# General Combining Ability Model for Genomewide Selection: Accuracy, Marker Imputation, and Genetic Diversity within Maize Biparental Populations

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**Abstract**

A general combining ability (GCA) model enables genomewide selection in the cross between parents A and B before the A/B cross itself is phenotyped. Prior A/* and */B populations, where * indicates any other parent, are used as the training population in the GCA model. I conducted three studies that utilized phenotypic data (grain yield, moisture, and test weight) and single nucleotide polymorphism data for 969 A/B crosses in the Monsanto maize (*Zea mays* L.) breeding program. The first study aimed to determine if the GCA model is useful for genomewide selection in an A/B cross, and to assess the influence of training population size, number of crosses in the training population, linkage disequilibrium, and heritability on the prediction accuracy ($r_{MP}$) with the GCA model. Increases in each of these factors improved the prediction accuracy. The GCA model led to selection responses (R) that were 68 to 76% of those eventually achieved with phenotypic selection. The second study aimed to determine: (i) if marker imputation increases R and $r_{MP}$ within biparental crosses; (ii) the number of markers needed to reach a plateau in $r_{MP}$; and (iii) the lowest number of assayed SNP markers that can be used for imputation without a significant decrease in $r_{MP}$. Marker imputation made the GCA model as good as or better than the A/B model (which used the A/B cross itself) in terms of R and $r_{MP}$. The $r_{MP}$ values did not increase significantly beyond 500 imputed markers for grain yield, and 1000 imputed markers for moisture and test weight. The third study aimed to determine if genomewide selection and phenotypic selection lead to comparable losses in genetic diversity within a biparental population. Phenotypic selection for grain yield, moisture, and an index of these two traits did not cause a significant loss in genetic diversity

among the selected lines. Genomewide selection of the best 5% of lines led to a small but statistically significant loss in genetic diversity. Overall, my results suggest that the GCA model is effective for genomewide selection within an A/B cross, prior to phenotyping the progeny in the cross itself.

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# Chapter 1: General combining ability model for genomewide selection in a biparental cross

Genomewide selection within an A/B biparental cross is most advantageous if it could be effectively done before the cross is phenotyped. Our objectives were to determine if a general combining ability (GCA) model is useful for genomewide selection in an A/B cross, and to assess the influence of training population size ($N_{GCA}$), number of crosses pooled into the training population ($N_X$), linkage disequilibrium ($r^2$), and heritability ($h^2$) on the prediction accuracy with the GCA model. The GCA model involved pooling 4–38 maize (*Zea mays* L.) crosses with A and B as one of the parents into the training population for an A/B cross, whereas the same background (SB) model involved pooling crosses between random inbreds. Across 30 A/B test populations, the mean response to selection (R) with the GCA model was 0.19 Mg ha$^{-1}$ for testcross grain yield, –6 g kg$^{-1}$ for moisture, and 0.38 kg hL$^{-1}$ for test weight. These R values with the GCA model were 68–76% of the corresponding R values with phenotypic selection. The R values with the SB model were only 15–28% of the R values with phenotypic selection. Increasing the size of the training population with random crosses from the same heterotic group was less important than including crosses with A and B as one of the parents. Prediction accuracy was most highly correlated with $h^2 r^2 \sqrt{N_{GCA}}$ and $h^2 r^2 \sqrt{N_X}$. Our results indicated that the GCA model is routinely effective for genomewide selection within A/B crosses, prior to phenotyping the progeny in the cross.

## Introduction

Maize (*Zea mays* L.) breeding typically involves crossing two inbreds (parent A and parent B), developing selfed or doubled haploid progeny from the A/B cross, and evaluating the progeny based on their yield and agronomic performance when crossed to a tester. Parents A and B are typically from the same heterotic group, whereas the tester is an inbred from an opposite heterotic group. Each A/B testcross population is developed and analyzed separately from other biparental testcross populations. Traditionally, testcross selection within a biparental cross has been based solely on phenotypic information (Hallauer, 1990).

Advances in single nucleotide polymorphism (SNP) genotyping have drastically lowered the cost of obtaining high quality marker information. With the advent of cheap and quick genotyping, genomewide selection (or genomic selection) has been introduced (Meuwissen et al., 2001) and studied (Bernardo and Yu, 2007; Heffner et al., 2009; Lorenz et al., 2011; Heslot et al., 2012) as a method for predicting performance for complex traits. In genomewide selection, marker effects are estimated from phenotypic and marker data in a training population. The marker effects are then used to predict the performance of a test population that has been genotyped but not phenotyped.

The training population must be representative of the test population to obtain a high prediction accuracy. In theory, the best training population for an A/B population is a subset of the A/B population that has been phenotyped and genotyped (i.e., the population itself). In this article, the use of a subset of A/B as a training population for A/B itself is referred to as the A/B model. Due to the need to phenotype a subset of A/B as the training

population, the A/B model increases the time and cost before genomewide selection can be performed within a biparental cross.

To eliminate the need to phenotype the A/B population itself, pooling multiple biparental crosses into a training population has been proposed (Schulz-Streeck et al., 2012; Zhao et al., 2012; Riedelsheimer et al., 2013). These multiple biparental crosses need to be of the same genetic background as A/B and need to have been previously genotyped and phenotyped. In a few studies, pooling multiple crosses into a training population was found to be superior to the A/B model (Schulz-Streeck et al., 2012; Zhao et al., 2012). The increase in prediction accuracy was likely due to the increase in the number of individuals in the training population when multiple biparental crosses were pooled (Schulz-Streeck et al., 2012).

The accuracy of genomewide prediction may be increased if identity by descent between the markers in the A/B test population and in the biparental crosses pooled into a training population is guaranteed. Suppose that * is any inbred that is in the same heterotic group as A and B, that the same tester is used for all biparental crosses, and that the SNP markers analyzed are those that are polymorphic between A and B. If all available A/* crosses are pooled into a training population, a SNP allele for which an effect is estimated in the training population (marker allele carried by parent A in the pooled A/* biparental crosses) will be identical by descent to the corresponding SNP allele unique to A in the A/B test population. Likewise, if all available */B crosses are pooled into a training population, a SNP allele for which an effect is estimated in the training population (marker allele carried by parent B in the pooled */B biparental crosses) will be identical by descent to the corresponding SNP allele unique to B in the A/B test population.

To predict the performance within an A/B test population, pooling all available A/* and */B biparental crosses into a training population for A/B is, therefore, likely to be superior to pooling multiple */* crosses into a training population; the latter having been proposed and studied previously (Schulz-Streeck et al., 2012; Zhao et al., 2012). In this article, we refer to pooling the A/* and */B biparental crosses as the general combining ability (GCA) model because the model captures GCA effects of marker alleles. In the plant breeding literature, GCA pertains to the mean performance of an inbred when crossed with a series of other inbreds. Similarly, the GCA model in this study estimates the trait mean of a SNP allele in combination with SNP alleles from other inbreds. We refer to pooling multiple */* crosses as the same background (SB) model.

In this study, we utilized a subset from 969 biparental maize populations to test the usefulness of the GCA model compared with the A/B and SB models. We also compared these models to phenotypic selection (PS) and to a combined SB+GCA model. The data were for actual breeding populations from Monsanto from 2001 to 2008 and were therefore representative of the pedigree backgrounds, range of genetic diversity, population sizes, and extent of field testing that may be encountered in a commercial maize breeding program. Our objectives in this study were to (i) determine if the GCA model is useful for genomewide selection in an A/B cross, and (ii) assess the influence of training population size ($N_{GCA}$), number of crosses pooled into the training population ($N_X$), linkage disequilibrium ($r^2$), and heritability ($h^2$), on the prediction accuracy with the GCA model.

## Materials and Methods

### *Test Populations*

Phenotypic and marker data for 969 biparental testcross populations were provided to us by Monsanto. A total of 485 crosses were between inbreds from one heterotic group (Group 1) and 485 crosses were between inbreds from an opposite heterotic group (Group 2). Individuals in each of the 969 populations were testcrossed to an inbred from the opposite heterotic group. From the 969 biparental crosses, we chose 30 A/B testcross populations as the test populations for the A/B, GCA, SB, and SB+GCA models as well as for PS (Table 1). The 30 A/B test populations were chosen based on having a minimum population size of 50 individuals, a minimum of four A/* and */B crosses, and a significant $V_G$. All pedigrees in the dataset were coded by Monsanto to protect confidentiality.

Two of the 30 A/B test populations were $BC_1$ populations, whereas the remaining 28 were $F_2$ populations. The 30 A/B test populations had 139–186 individuals (Table 1). Testcrosses of these individuals were evaluated for grain yield (Mg $ha^{-1}$), moisture (g $kg^{-1}$), and test weight (kg $hL^{-1}$) at 4–12 environments (year-location combinations) in the U.S. from 2001 to 2008. Phenotypic data were available as the mean of each individual within each location. Phenotypic data on some of the individuals were missing from some locations, making the phenotypic data unbalanced. All phenotypic data were at the testcross level, and the same tester was used for an A/B test population and for the training population used to predict the performance of the A/B cross. The use of the same tester eliminated confounding effects, due to different testers, in the performance of each set of A/B, A/*, */B, and */* crosses for which comparisons were made. However, different testers were used across the 30 A/B test populations (Table 1).

Testcross genetic variance ($V_G$) and heritability on an entry-mean basis ($h^2$) were estimated for each trait in all 969 populations. Restricted maximum likelihood estimates of variance components were obtained with the lme4 package (Bates, 2011) in R statistical software (R Development Core Team, 2012; Holland, 2003). A likelihood ratio test was used to determine the significance of the estimates of $V_G$. The *p*-value from the likelihood ratio test was divided by 2.0 to approximate an F-test of the null hypothesis (Holland et al., 2003). A $V_G$ estimate with a *p*-value less than 0.05 was considered significant. Across the 30 A/B crosses, the percentage of missing data (i.e., individual-location combinations) had a mean of only 2% and a maximum of 5% for each trait. The $h^2$ was estimated on an ad hoc basis as $h^2 = V_G/(V_G + V_R/e)$, where $V_R$ was the residual variance and $e$ was the mean number of environments. Because the data were entry means within each location, the genotype by environment interaction variance and within-location error variance were confounded in $V_R$. The value of $e$ was estimated as the harmonic mean, given the unbalanced nature of the data (Holland, 2003). The 30 A/B test populations were chosen based on having a minimum population size of 50 individuals, a minimum of four total A/* and */B crosses, and a significant $V_G$.

The parents of the A/B test populations were genotyped with 2911 SNP markers, whereas the individuals within each A/B cross were genotyped with 49 to 100 SNP markers that were polymorphic between A and B. The A/B populations with lower numbers of markers tended to be those whose parents were more similar based on the 2911 SNP markers. The linkage disequilibrium (LD) was calculated as the mean $r^2$ values between adjacent SNP markers with R statistical software (R Development Core Team, 2012). As

with the pedigree data, the names of the SNP markers were coded by Monsanto to protect confidentiality.

As described in further detail below, the different models for designing training populations were compared based on two criteria: (i) the response to selection (R) in each A/B test population, and (ii) the correlation between marker-predicted performance and observed performance ($r_{MP}$) in each A/B test population.

*A/B Model*

In the A/B model, the individuals in the test population and the individuals in the training population were from the same A/B cross. The value of $r_{MP}$ was calculated through a delete-one procedure along with cross-validation across environments.

With $N$ individuals in an A/B cross, the performance of the first individual was predicted by ridge regression-best linear unbiased prediction (RR-BLUP) analysis of the effects of $N_M$ total markers among the remaining $N - 1$ individuals. Given the low incidence of missing data, arithmetic means of the individuals across locations were used in RR-BLUP (i.e., with no correction for missing data); this procedure facilitated the cross-validation across environments as described in the next paragraph. The R package rrBLUP version 4.0 in R statistical software (Piepho, 2009; Endelman, 2011; R Development Core Team, 2012) was used to estimate the marker effects. For each trait, the performance of the first individual was predicted as $y_P = \mu + \mathbf{xg}$, where $y_P$ was the predicted performance of the individual; $\mu$ was the estimated mean of the $N - 1$ individuals used as the training population; $\mathbf{x}$ was a $1 \times N_M$ row vector of genotype indicators; and $\mathbf{g}$ was a $N_M$ x 1 vector of RR-BLUP marker effects, estimated from the remaining $N - 1$ individuals, for the SNP alleles from the first parent. The elements of $\mathbf{x}$ were 1 if the test individual was homozygous

for the SNP allele from parent A, –1 if the test individual was homozygous for the SNP allele from parent B, and 0 if the test individual was heterozygous. The delete-one analysis was sequentially repeated with the performance of the second individual being predicted from the remaining $N$ – 1 individuals, the performance of the third individual being predicted from the remaining $N$ – 1 individuals, and so on. In the end, the performance of each of the N individuals was predicted from the remaining $N$ – 1 individuals.

The above cross-validation was conducted across environments to eliminate a bias, present in the A/B model but not in the other models, due to the test population and training population being evaluated in the same environments. In this procedure, RR-BLUP marker effects were estimated from the performance of the $N$ – 1 individuals in half of the environments. These marker effects were then used to predict the performance of the test individual in the remaining half of the environments.

For example, there were 20 combinations of three out of six environments. The delete-one RR-BLUP marker effects were then obtained for each of these 20 combinations, and the marker effects for each combination were used to obtain $y_P$ for each of the $N$ individuals as described above. For each of the 20 combinations, $r_{MP}$ was obtained as the correlation between $y_P$ and the mean performance of each of the $N$ individuals in the remaining half of the environments that were not used to calculate marker effects. The mean $r_{MP}$ across all 20 combinations was obtained. The same procedure was used for larger numbers of environments. When the number of environments (e) was an odd number, (e−1)/2 environments were used to estimate marker effects and the observed performance of each of the $N$ individuals was based on the remaining environments.

The values of R for high grain yield, low moisture, and high test weight were obtained as follows. Again, suppose that an A/B population was evaluated in six environments. For each of the 20 combinations, the 10% of individuals with the best $y_P$ values were identified for each trait. The mean observed performance of these individuals in the other half of the environments was obtained and was denoted as $y_{0.10}$. The R for each of the 20 combinations was then estimated as $y_{0.10} - \mu$. The final value of R was then obtained as the mean R across the 20 combinations. Simulations we have conducted (results not shown) have confirmed that this procedure is valid for estimating R, and that the estimated value does not correspond to the selection differential.

The variances of $r_{MP}$ and R were obtained across the different repeats of the cross-validations across environments. These variances were then used to calculate LSD values ($P = 0.05$) for the mean $r_{MP}$ and mean R.

*General Combining Ability Model*

The GCA model is based on the premise that effects of the two alleles at a SNP locus in an A/B cross can be sufficiently modeled as (i) the mean of effects (denoted by $m_{A\_}$) of a SNP marker in parent A when A is crossed with multiple inbreds, and (ii) the mean of effects (denoted by $m_{B\_}$) of a SNP marker in parent B when B is crossed with multiple inbreds. Suppose that $m_{A/B}$ is the testcross effect of the SNP allele from parent A within the A/B cross. Likewise, $m_{B/A}$ is the testcross effect of the SNP allele from parent B within the A/B cross. The marker effects are $m_{A/B} = m_{A\_}$ + residual and $m_{B/A} = m_{B\_}$ + residual. The GCA model ignores the residuals, which are specific to the A/B combination and which cannot be estimated unless A/B itself is evaluated.

In the GCA model, the number of A/* and */B crosses that were pooled into a training population ($N_X$) for each A/B test population ranged from 4 to 38 (Table 1). The total size of the pooled training population ($N_{GCA}$) ranged from 634 to 5255 individuals, all with the same tester as the A/B population (Table 1). The number of polymorphic SNP markers used to genotype the A/* and */B crosses ranged from 38 to 116 and had a mean of 74.

Because different sets of SNP markers were used in different populations, each A/* and */B cross was analyzed separately to obtain RR-BLUP marker effects within each cross. For a given trait, the performance of all $N$ individuals in the A/B test population was predicted as $\mathbf{y} = \mu\mathbf{1} + \mathbf{Xm}$, where **y** was an $N \times 1$ vector of predicted performance; μ was the estimated overall mean; **1** was an $N \times 1$ vector with elements equal to 1; **X** was an $N \times N_M$ matrix of genotype indicators with elements of 1, –1, and 0 (same as for **x**); and **m** was an $N_M$ x 1 vector of RR-BLUP marker effects averaged across the A/* and */B crosses. All markers in each A/* and */B cross were used in RR-BLUP analysis within the cross. However, the $N_M$ for obtaining **y** referred to the markers in the A/B test population. Markers in the A/B test population were removed if they were not present in at least two A/* or */B crosses. The separate RR-BLUP analyses for each A/* and */B cross inherently accounted for population structure, with the fitted values of μ differing among the A/* and */B crosses and thereby reflecting population structure.

We studied two versions of the GCA model that differed in how **m** was calculated. In the GCA model, marker effects were estimated as the unweighted mean across all A/* and */B crosses in which a particular marker was polymorphic. Suppose the training population was obtained by pooling 10 A/* crosses and 12 */B crosses and that all 22

crosses were polymorphic for SNP1, which was also polymorphic in A/B. Further suppose that parent A had the T allele and parent B had the C allele at the SNP1 locus. With biallelic SNPs, this means that the * parents in the 10 A/* crosses carried the C allele, and the * parents in the 12 */B crosses carried the T allele. In the GCA model, the effect of the T marker allele at SNP1 was the unweighted mean of the estimated marker effects of the T allele in all 22 crosses. Likewise, the effect of the C marker allele of SNP1 was the unweighted mean of the estimated marker effects of the C allele in all 22 crosses.

Not all SNP markers in the A/B cross were polymorphic in all of the A/* and */B crosses. With the previous example, suppose that SNP2 was not polymorphic in the last two */B crosses. In this situation, the mean marker effects at SNP1 were obtained from all 10 A/* and 12 */B crosses, whereas the mean marker effects at SNP2 were obtained from all 10 A/* crosses and the first 10 */B crosses.

In the $GCA_{IBD}$ model, the effect of the T marker allele at SNP1 (found in parent A) was the unweighted mean of the estimated marker effects of the T allele in the 10 A/* crosses only. Likewise, the effect of the C marker allele of SNP1 (found in parent B) was the unweighted mean of the estimated marker effects of the C allele in the 12 */B crosses only. The $GCA_{IBD}$ model, therefore, guaranteed that estimates of mean marker effects were obtained only from those crosses where identity by descent (IBD) is guaranteed between a marker allele in the A/B cross and in the training population.

For the GCA model and $GCA_{IBD}$ model, the values of $r_{MP}$ and R were calculated in the same way as for the A/B model. Cross-validation across environments was done for the A/B test population according to the same procedure for splitting environments used in the A/B model. However, data from all environments were always used in estimating

marker effects within the A/* and */B populations, which were evaluated in sets of environments that were different from those used to evaluate the A/B cross.

*Same Background Model*

In the SB model, the number of randomly selected */* crosses that were pooled into a training population for each A/B test population was equal to that for the GCA model. The total size of the pooled training population ($N_{SB}$) in the SB model was kept generally similar to that in the GCA model and ranged from 615 to 5647 individuals. The number of polymorphic SNP markers used to genotyped the */* crosses ranged from 59 to 84 and had a mean of 73.

In the SB+GCA model, the training population for an A/B cross comprised all the A/* and */B crosses from the GCA model and all the */* crosses from the SB model. The procedures for calculating R and $r_{MP}$ with the SB model and SB+GCA model were the same as those for the GCA model and $GCA_{IBD}$ model.

*Phenotypic Selection*

In PS, the mean performance of an A/B individual in half of the environments was considered as the predictor of the performance of the same individual in the remaining half of the environments. Procedures for calculating the prediction accuracy of PS and R were the same as those used for $r_{MP}$ and R in the GCA, SB, and SB+GCA models. For convenience, the prediction accuracy with PS was also denoted as $r_{MP}$ in Tables 2–5 even though the prediction of performance with PS did not involve marker effects.

*Genetic Similarity Thresholds*

We investigated the effect in the GCA model of imposing a minimum similarity between the * parents and the A and B parents. Genetic similarity was calculated (i) between parent A and the * inbred from the */B cross ($S_{A*}$), and (ii) between parent B and the * inbred from the A/* cross ($S_{B*}$). The genetic similarity was calculated as the simple matching coefficient (Sokal and Michener, 1958) across 2911 SNP markers that were used to screen all the parents.

The A/* and */B crosses in the GCA model were then restricted to those in which the values of $S_{A*}$ and $S_{B*}$ both exceeded threshold values of 0.60, 0.70 or 0.80. Values of $r_{MP}$ and R were calculated as described for the GCA model.

## Results and Discussion

*Models for Predicting Performance within an A/B Cross*

Based on the mean R and mean $r_{MP}$ across the 30 A/B test populations (Table 2), the overall ranking of the six models we studied was as follows: PS > A/B > GCA > $GCA_{IBD}$ > GCA+SB > SB. The overall ranking of the models was the same for the three traits we studied (grain yield, moisture, and test weight). However, the ranking of the six methods was not always the same across the 30 test populations (Tables 3–5).

The predictions were expected to be most accurate when they were made from within the population itself. Predictions with PS and the A/B model were based on the performance of the A/B test population itself, and the superiority of PS and of the A/B model was, therefore, consistent with expectations. Phenotypic selection had the highest mean R for grain yield (0.25 Mg $ha^{-1}$), moisture (–7 g $kg^{-1}$), and test weight (0.56 kg $hL^{-1}$)

(Table 2). Phenotypic selection also had the highest mean $r_{MP}$ for all three traits (0.24 for grain yield, 0.44 for moisture, and 0.34 for test weight). Although the differences between the two methods were mostly nonsignificant ($P$ = 0.05), the mean R and $r_{MP}$ values were consistently lower with the A/B model than with PS. Across the three traits, mean R values with the A/B model were 72–86% of the R values with PS. As expected, the mean R and $r_{MP}$ values within a trait were highly correlated across the six models we studied (correlations of 0.95 for grain yield, 0.98 for moisture, and 0.99 for test weight).

The values of the prediction accuracy with PS indicated that the correlation between the testing environments was low to moderate. Quantitative traits are strongly influenced by genotype by environment interaction, which leads to the genotypes reacting differently in different environments (Haldane, 1946; Cooper and Delacy, 1994). While genotype by environment interaction variance could not be estimated with the data in this study, genotype by environment interaction in maize is usually strong (Ouyang et al., 1995) and it necessitates the testing of maize hybrids across multiple environments.

It is advantageous to predict the performance of individuals within an A/B cross prior to phenotyping the cross itself, which is required in PS and in the A/B model. In the GCA model, the training population was constructed by pooling previously phenotyped crosses with A and B as one of the parents. The mean R with the GCA model was 0.19 Mg $ha^{-1}$ for grain yield, –6 g $kg^{-1}$ for moisture, and 0.38 kg $hL^{-1}$ for test weight (Table 2). The mean $r_{MP}$ was 0.14 for grain yield, 0.32 for moisture, and 0.24 for test weight (Table 2). Across the three traits, mean R values with the GCA model were 68–76% of the R values with PS. Compared with the A/B model, the GCA model had statistically equal or slightly lower mean R and $r_{MP}$.

One important advantage of PS over genomewide selection was that responses to selection were always in the favorable direction with PS. In contrast, the five genomewide selection models had instances of responses in the unfavorable direction. For grain yield, all of the R values were all positive for PS, but three populations had a negative R with A/B model and four populations had a negative R with the GCA model (Table 3). The unfavorable gains may have been due to associations between SNPs and QTL that were not conserved among populations (Liu et al., 2011; Zhao et al., 2012).

The mean R and mean $r_{MP}$ values were lower with the $GCA_{IBD}$ model than with the GCA model for all three traits (Table 2). The small but consistent reductions in R and $r_{MP}$ with the $GCA_{IBD}$ model may have occurred because the marker effects was estimated from fewer crosses in the $GCA_{IBD}$ model than in the GCA model. For example, in population P24/P26, eight A/* and 14 */B crosses were pooled into the training population. Marker effects in the GCA model were, therefore, estimated from 22 crosses, whereas marker effects in the $GCA_{IDB}$ model were estimated from eight crosses (marker effects for P24) and 14 crosses (marker effects for P26).

In the GCA model, increasing the level of genetic similarity between the * parent and the A/B cross did not improve the predictions. We found no significant difference ($P = 0.05$) in R and $r_{MP}$ when the training populations only included A/* and */B crosses for which the values of $S_{A*}$ and $S_{B*}$ both exceeded threshold values of 0.60, 0.70 or 0.80. The influence of genetic similarity was confounded with changes in the size of the training population, because higher thresholds for genetic similarity reduced the number of crosses that could be included in the training population. However, the R and $r_{MP}$ were similar even as the population size greatly decreased due to removing populations below the genetic

similarity threshold. This result suggested that the contributions of the A and B parents themselves (in the A/* and */B crosses) may be providing most of the information for predictions in the GCA model. Previous studies have shown that $r_{MP}$ decreased when the relationship between the training and test population was weak, especially when the training population was small (Habier et al., 2010; Asoro et al., 2011; Clark et al., 2012). However, the use of crosses that have A and B as one of the parents inherently leads to a strong relationship between the training and test population, to the extent that previous results that focus on weaker relatedness do not apply.

The SB model was ineffective even though (i) the crosses pooled into the training population were from the same heterotic group as the A/B cross, (ii) the number of crosses pooled into a training population was equal between the SB and GCA models, and (iii) the size of the training population was roughly the same between the SB and GCA models (Table 1). The mean $r_{MP}$ across the three traits was only 0.06–0.11 with the SB model, and the R with SB model was only 15–28% of the R with PS (Table 2). These results were inconsistent with several previous studies that showed combining multiple related populations (Schulz-Streeck et al., 2012; Zhao et al., 2012; Windhausen et al., 2012) or multiple populations from opposite heterotic groups (Technow et al., 2013) improved the prediction accuracy over the A/B model, but they were consistent with one previous study that showed that including populations with the same genetic background can cause a lower or even negative prediction accuracy (Riedelsheimer et al., 2013). This result may have been due to opposite linkage phases between the QTLs in the training and test populations (Lorenz et al., 2012; Riedelsheimer et al., 2013).

Increasing the size of the training population has been previously found to be an important factor in increasing the prediction accuracy (Heffner et al., 2011a). Compared with the GCA model, the SB+GCA model had double the number of crosses in the training population and roughly double the size of the training population. However, the GCA model was as effective or more effective than the SB+GCA model. While the differences were often nonsignificant, the mean R and $r_{MP}$ values were consistently lower with the SB+GCA model than with the GCA model (Table 2). Increasing the size of the training population with random populations is, therefore, less important than including A/* and */B crosses in the training population for the A/B cross. Similar results were found by Riedelsheimer et al. (2013).

*Influence of Heritability, Linkage Disequilibrium, Size of the Training Population, and Number of Markers on the GCA Model*

The $h^2$ values for grain yield, moisture, and test weight varied widely among the 30 test populations (Table 1). While the mean $h^2$ was 0.38 for grain yield, 0.66 for moisture, and 0.53 for test weight, the $h^2$ within a test population ranged from 0.20 to 0.62 for grain yield (Table 3), 0.38 to 0.85 for moisture (Table 4), and 0.27 to 0.83 for test weight (Table 5). With the GCA model, the correlation between $h^2$ and $r_{MP}$ was positive for each trait but was significant only for moisture (Table 6).

The 30 A/B test populations differed widely in the number of individuals in the training population for the GCA model ($N_{GCA}$). However, the $N_{GCA}$ was always large, ranging from 634 to 5255 (Table 1). With the GCA model, the correlations between $N_{GCA}$ and $r_{MP}$ were positive but significant only for moisture (Table 6). Our results agree with previous studies that indicated that an increase in $N$ results in an increase in $r_{MP}$ (Lorenzana

and Bernardo, 2009; Asoro et al., 2011; Heffner et al., 2011a; b; Guo et al., 2012; Lorenz et al., 2012).

The expected prediction accuracy ($r_{MG}$) is a function of $\sqrt{N_{GCA}h^2}$ instead of $N_{GCA}$ and $h^2$ individually (Daetwyler et al., 2010). Because $r_{MP}$ is equal to $r_{MP}h$, $r_{MP}$ is a function of $h^2\sqrt{N_{GCA}}$. Our empirical results were consistent with this theoretical result from Daetwyler et al. (2010), with the correlation between $r_{MP}$ and $h^2\sqrt{N_{GCA}}$ for the GCA model being significant for moisture and test weight but not for grain yield (Table 6). These results generally agree with previous research that found that within the same trait, the product of $Nh^2$ is more important than $N$ and $h^2$ evaluated individually (Combs and Bernardo, 2013a).

We have previously found that the Daetwyler (2010) equation for prediction accuracy can be modified by incorporating information on LD ($r^2$) between adjacent markers (Lian et al., 2014). The correlation between $r_{MP}$ and $h^2r^2\sqrt{N_{GCA}}$ was 0.36 for grain yield, 0.58 for moisture, and 0.48 for test weight (Table 6). The higher correlations of $r_{MP}$ with $h^2r^2\sqrt{N_{GCA}}$ than with $h^2\sqrt{N_{GCA}}$ indicated that when the genome is unsaturated with markers, mean $r^2$ values contribute to the expected prediction accuracy (Lian et al., 2014).

In addition to the large variability in the number of individuals in the training population, there was also a large variability in the number of crosses that comprised the training population for the GCA model ($N_X$). The correlation between $N_X$ and $r_{MP}$ was significant for moisture and test weight but not for grain yield (Table 6). The training populations with the most A/* and */B crosses tended to have the largest R values. For example, in the P21/P22 population, 38 A/* and */B crosses were used in the training

population, and R was high at 0.37 Mg ha$^{-1}$ for grain yield (Table 3), -7 g kg$^{-1}$ for moisture (Table 4), and 0.87 kg hL$^{-1}$ for test weight (Table 5).

As with $h^2\sqrt{N_{GCA}}$, the correlations between $r_{MP}$ and $h^2\sqrt{N_X}$ were higher than the correlations with $N_X$ and $h^2$ evaluated individually (Table 6). These correlations were increased further by incorporating LD. The correlations between $r_{MP}$ and $h^2r^2\sqrt{N_X}$ were 0.31 for grain yield, 0.57 for moisture and 0.52 for test weight (Table 6). Further studies are needed to evaluate the effect of increasing $N_X$ while keeping $N_{GCA}$ constant or of increasing $N_{GCA}$ and while keeping $N_X$ constant. On the other hand, knowledge of the independent effects of $N_{GCA}$ and $N_X$ would be of little practical value because, in practice, $N_{GCA}$ and $N_X$ would tend to be highly correlated.

The correlation between the number of markers ($N_M$) and $r_{MP}$ was not significant for any of the traits (Table 6). Previous studies have indicated that $r_{MP}$ increases as the $N_M$ increases, but $r_{MP}$ plateaus once the genome is covered with markers (Lorenzana and Bernardo, 2009; Asoro et al., 2011; Heffner et al., 2011a; b; Guo et al., 2012; Combs and Bernardo, 2013a). Large chromosomal segments are passed intact from parents to progeny in a biparental cross, to the extent that markers spaced 10–15 cM are largely sufficient (R. Bernardo, unpublished data, 2013) for genomewide selection within a biparental cross. Finding many polymorphic markers can also be difficult in crosses between related elite inbreds, such as those in this study. The mean $r^2$ between adjacent markers across the 30 populations was 0.51 with a range of 0.36-0.64 (Table 1), and the mean $r^2$ among all 969 populations (0.46) was likewise high. The high $r^2$ values indicated that although marker coverage is low there was substantial LD for genomewide selection. A previous study in maize found that genomewide selection was still effective when the $r^2$ was as low as 0.26-

0.35 (Massman et al., 2013). Nevertheless, increasing the number of markers may help increase the R and $r_{MP}$ for the GCA, A/B, SB and SB+GCA models.

Overall, $h^2 r^2 \sqrt{N_{GCA}}$ and $h^2 r^2 \sqrt{N_X}$ were the two criteria with the highest correlations with $r_{MP}$ and for which the correlations were significant across all three traits, except for $h^2 r^2 \sqrt{N_X}$ for grain yield (Table 6). These two criteria should therefore be the ones used for designing genomewide selection programs with the GCA model. When prediction accuracy is expressed as $r_{MG}$ instead of $r_{MP}$, the corresponding criteria would be $r^2 \sqrt{h^2 N_{GCA}}$ and $r^2 \sqrt{h^2 N_X}$ .

*Implications in Inbred Development*

Our results show that selection within an A/B cross is most effective when selection decisions—made from either field data (PS) or marker-based predictions (A/B model)—are based on the performance of the A/B cross itself. But PS and the A/B model are highly time consuming and expensive because the A/B population itself needs to be phenotyped. Time and cost are particularly limiting in inbred development that does not involve recurrent selection; in the latter, the time and cost in phenotyping can be justified by the increase in the gain per unit time when multiple cycles of genomewide selection are performed in a year-round nursery or greenhouse (Massman et al., 2012; Combs and Bernardo, 2013b).

The GCA model led to the highest R and $r_{MP}$ among the models that eliminate the need to phenotype the A/B test population itself. The GCA model relies on information from previously phenotyped and genotyped crosses with inbreds A and B as one of the parents and is conducive in advanced breeding programs that use elite inbreds as the

parents of new breeding crosses. In the context of inbred development, genomewide selection with the GCA model seems most useful during the stages of the breeding program when gains from phenotypic selection are zero or are low. In particular, the evaluation of individual $F_2$ plants *per se* has a low genetic correlation with the testcross performance of the $F_2$ plant or of an inbred derived from the $F_2$ plant when heterosis is substantial and when heritability is low (Smith, 1986; Bernardo, 1991b; Mihaljevic et al., 2004). Current gains for hybrid grain yield from any mass selection for grain yield among individual $F_2$ plants are, therefore, probably zero or close to zero. Our results indicated that, on average, genomewide selection with the GCA model among $F_2$ plants in an A/B cross would lead to single-trait gains of 0.19 Mg $ha^{-1}$ (or 3 bushels per acre) for grain yield, –6 g $kg^{-1}$ (or –0.6%) for moisture, and 0.38 kg $hL^{-1}$ (or 0.30 lb per bushel) for test weight (Table 2). These gains were 68–76% of the corresponding gains with phenotypic selection based on testcross performance in replicated experiments and could be achieved at a fraction of the cost of phenotypic selection.

Table 1: Test and training populations for the A/B, general combining ability (GCA) and same background (SB) models in maize.

| | Test population | | | | | | | | | GCA model | | | | SB model |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | $N_M$[†] | | | | Populations | | | | |
| Group[‡] | A/B population | Tester | $S_{A/B}$[§] | $N$[¶] | Locations | A/B | GCA | SB | SB+GCA | A/* | */B | $N_x$[#] | $N_{GCA}$[††] | $N_{SB}$[‡‡] |
| 1 | P1/P2 | T1 | 0.79 | 152 | 7 | 79 (0.62) | 79 | 79 | 79 | 23 | 15 | 38 | 5255 | 5178 |
| 1 | P3/P4 | T1 | 0.74 | 164 | 8 | 58 (0.43) | 47 | 55 | 58 | 11 | 17 | 28 | 4530 | 4419 |
| 1 | P4/P5 | T1 | 0.66 | 177 | 6 | 82 (0.49) | 78 | 70 | 78 | 17 | 8 | 25 | 3858 | 3772 |
| 1 | P6/P7 | T1 | 0.59 | 183 | 12 | 67 (0.44) | 66 | 63 | 66 | 17 | 5 | 22 | 3295 | 3225 |
| 1 | P3/P8 | T1 | 0.74 | 181 | 7 | 69 (0.51) | 62 | 63 | 65 | 11 | 5 | 16 | 2800 | 2787 |
| 1 | P1/P9 | T2 | 0.82 | 174 | 5 | 74 (0.63) | 68 | 68 | 68 | 7 | 8 | 15 | 1874 | 1961 |
| 1 | P5/P8 | T1 | 0.61 | 148 | 6 | 74 (0.36) | 64 | 64 | 68 | 9 | 4 | 13 | 1724 | 1796 |
| 1 | P9/P10 | T2 | 0.85 | 152 | 8 | 68 (0.58) | 63 | 63 | 64 | 9 | 4 | 13 | 1724 | 1796 |
| 1 | P9/P2/P9 | T2 | 0.79 | 159 | 6 | 87 (0.60) | 67 | 63 | 79 | 8 | 5 | 13 | 2022 | 1958 |
| 1 | P11/P12 | T1 | 0.62 | 182 | 8 | 91 (0.45) | 53 | 60 | 77 | 2 | 9 | 11 | 1325 | 1421 |
| 1 | P13/P14 | T3 | 0.76 | 178 | 8 | 86 (0.64) | 82 | 60 | 84 | 7 | 3 | 10 | 1688 | 1620 |
| 1 | P2/P15 | T3 | 0.68 | 160 | 5 | 89 (0.57) | 68 | 75 | 81 | 5 | 4 | 9 | 1477 | 1496 |
| 1 | P16/P13 | T3 | 0.83 | 178 | 7 | 53 (0.59) | 47 | 39 | 50 | 7 | 2 | 9 | 1541 | 1468 |
| 1 | P17/P18 | T1 | 0.70 | 185 | 7 | 87 (0.50) | 54 | 51 | 67 | 2 | 4 | 6 | 793 | 758 |
| 1 | P19/P20 | T4 | 0.64 | 186 | 5 | 100 (0.52) | 67 | 39 | 77 | 1 | 3 | 4 | 697 | 615 |
| 2 | P21/P22 | T5 | 0.82 | 173 | 8 | 69 (0.51) | 69 | 69 | 69 | 14 | 22 | 36 | 5168 | 5647 |
| 2 | P23/P24 | T6 | 0.84 | 174 | 7 | 49 (0.56) | 44 | 44 | 46 | 23 | 8 | 31 | 4199 | 5241 |
| 2 | P25/P22 | T5 | 0.77 | 169 | 8 | 72 (0.44) | 69 | 67 | 69 | 22 | 4 | 26 | 3960 | 4109 |
| 2 | P26/P27 | T6 | 0.76 | 184 | 6 | 66 (0.60) | 60 | 61 | 65 | 15 | 9 | 24 | 3550 | 3913 |
| 2 | P23/P25 | T5 | 0.73 | 168 | 7 | 68 (0.40) | 65 | 63 | 66 | 4 | 18 | 22 | 3188 | 3615 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2 | P24/P26 | T6 | 0.74 | 183 | 6 | 66 (0.47) | 66 | 66 | 66 | 8 | 14 | 22 | 1928 | 3255 |
| 2 | P28/P27 | T6 | 0.74 | 180 | 8 | 49 (0.43) | 48 | 43 | 49 | 9 | 4 | 13 | 1829 | 1984 |
| 2 | P29/P27 | T6 | 0.75 | 175 | 7 | 69 (0.56) | 61 | 59 | 69 | 4 | 9 | 13 | 1309 | 1930 |
| 2 | P29/P30 | T6 | 0.72 | 183 | 5 | 98 (0.53) | 77 | 54 | 63 | 4 | 6 | 10 | 1771 | 1363 |
| 2 | P31/P32 | T7 | 0.74 | 172 | 4 | 65 (0.46) | 57 | 31 | 56 | 2 | 8 | 10 | 1596 | 1692 |
| 2 | P33/P34 | T8 | 0.81 | 170 | 8 | 63 (0.39) | 57 | 53 | 58 | 3 | 6 | 9 | 1042 | 1495 |
| 2 | P35/P36 | T9 | 0.76 | 181 | 7 | 85 (0.60) | 54 | 54 | 64 | 4 | 2 | 6 | 634 | 1036 |
| 2 | P37/P38 | T10 | 0.78 | 139 | 4 | 62 (0.37) | 48 | 22 | 51 | 3 | 2 | 5 | 710 | 645 |
| 2 | P39/P40/P39 | T5 | 0.78 | 184 | 5 | 83 (0.44) | 60 | 31 | 52 | 3 | 2 | 5 | 650 | 715 |
| 2 | P41/P42 | T11 | 0.70 | 183 | 5 | 74 (0.50) | 58 | 48 | 59 | 2 | 2 | 4 | 650 | 625 |

†$N_{M,}$ number of markers used to estimate the performance of the A/B test population, markers for the GCA, SB, and SB+GCA models were removed if the marker was not present in at least two training populations. Mean $r^2$ of adjacent SNP markers is listed in parentheses for the A/B population.

‡Heterotic group.

§Simple matching coefficient between parents A and B.

¶$N$, number of individuals in the A/B test population.

#$N_X$, number of biparental crosses in the training population for the GCA and the SB model.

††$N_{GCA}$, number of individuals in the training population for the GCA model.

‡‡$N_{SB,}$ number of individuals in the training population for the SB model.

Table 2: Mean and range (in parentheses) of response to selection (R) and prediction accuracy ($r_{MP}$) across 30 test populations in maize.

| | Grain yield ($h^2$=0.38)[†] | | Moisture ($h^2$=0.66) | | Test weight ($h^2$=0.53) | |
|---|---|---|---|---|---|---|
| Method | R (Mg ha$^{-1}$) | $r_{MP}$ | R (g kg$^{-1}$) | $r_{MP}$ | R (kg hL$^{-1}$) | $r_{MP}$ |
| PS | 0.25$^{a‡}$ (0.03, 0.58) | 0.24$^{a}$ (0.05, 0.42) | -7$^{a}$ ( -15, -2) | 0.44$^{a}$ (0.21, 0.67) | 0.56$^{a}$ (0.04, 1.06) | 0.34$^{a}$ (0.07, 0.62) |
| A/B | 0.18$^{ab}$ (-0.15, 0.57) | 0.14$^{b}$ (-0.06, 0.39) | -6$^{a}$ ( -16, 1) | 0.38$^{a}$ (0.05, 0.67) | 0.44$^{ab}$ (0.06, 0.85) | 0.29$^{ab}$ (0.06, 0.60) |
| GCA | 0.19$^{ab}$ (-0.05, 0.52) | 0.14$^{b}$ (0.01, 0.40) | -6$^{a}$ (-13, 0) | 0.32$^{b}$ (-0.02, 0.53) | 0.38$^{bc}$ (-0.06, 0.87) | 0.24$^{bc}$ (-0.05, 0.48) |
| $GCA_{IBD}$ | 0.15$^{bc}$ (-0.10, 0.54) | 0.12$^{b}$ (-0.06, 0.31) | -4$^{b}$ (-9, 1) | 0.26$^{bc}$ (-0.02, 0.51) | 0.24$^{d}$ (-0.30, 0.74) | 0.18$^{cd}$ (-0.07, 0.39) |
| SB | 0.07$^{c}$ (-0.25, 0.50) | 0.06$^{c}$ (-0.13, 0.30) | -1$^{c}$ (-4, 4) | 0.11$^{d}$ (-0.07, 0.29) | 0.11$^{e}$ (-0.31, 0.75) | 0.07$^{e}$ (-0.07, 0.35) |
| SB+GCA | 0.17$^{b}$ (-0.11, 0.52) | 0.12$^{b}$ (-0.05, 0.44) | -4$^{b}$ (-8, 0) | 0.25$^{c}$ (-0.02, 0.49) | 0.29$^{cd}$ (-0.31, 0.91) | 0.17$^{d}$ (-0.23, 0.36) |
| LSD | 0.079 | 0.056 | 1.49 | 0.063 | 0.121 | 0.065 |

[†]Mean heritability ($h^2$) on an entry-mean basis.

[‡]Within a column, estimates with a common letter were not significantly different (P=0.05).

Table 3: Response to selection (R) and prediction accuracy ($r_{MP}$) for grain yield with phenotypic selection (PS) and with the A/B, general combining ability (GCA), GCA-identity by descent ($GCA_{IBD}$), same background (SB), and SB+GCA models for genomewide selection in maize.

| Test population | $h^{2\dagger}$ | R (Mg ha$^{-1}$) | | | | | | $r_{MP}$ | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | PS | A/B | GCA | $GCA_{IBD}$ | SB | SB+GCA | PS | A/B | GCA | $GCA_{IBD}$ | SB | SB+GCA |
| P1/P2 | 0.62 | 0.53 | 0.48 | 0.52 | 0.54 | 0.50 | 0.52 | 0.42 | 0.27 | 0.30 | 0.29 | 0.15 | 0.14 |
| P3/P4 | 0.31 | 0.29 | 0.10 | 0.15 | 0.20 | 0.22 | 0.21 | 0.19 | 0.05 | 0.09 | 0.14 | 0.11 | 0.13 |
| P4/P5 | 0.43 | 0.33 | 0.18 | 0.26 | 0.20 | 0.29 | 0.36 | 0.28 | 0.22 | 0.25 | 0.20 | 0.10 | 0.14 |
| P6/P7 | 0.50 | 0.27 | 0.30 | 0.11 | 0.12 | 0.04 | 0.11 | 0.28 | 0.26 | 0.10 | 0.04 | 0.03 | 0.09 |
| P3/P8 | 0.43 | 0.17 | 0.11 | 0.27 | -0.06 | -0.25 | 0.08 | 0.21 | 0.09 | 0.16 | -0.02 | -0.02 | 0.16 |
| P1/ P9 | 0.40 | 0.10 | 0.28 | 0.36 | 0.31 | 0.15 | 0.41 | 0.26 | 0.34 | 0.40 | 0.31 | 0.24 | 0.44 |
| P5/P8 | 0.34 | 0.41 | 0.45 | 0.40 | 0.36 | 0.02 | -0.08 | 0.26 | 0.30 | 0.17 | 0.26 | -0.04 | -0.01 |
| P9/P10 | 0.43 | 0.27 | 0.08 | -0.04 | 0.03 | 0.12 | 0.34 | 0.25 | 0.23 | 0.01 | $0.00^{NS\ddagger}$ | 0.30 | 0.23 |
| P9/P2/P9 | 0.43 | 0.58 | 0.57 | 0.42 | 0.33 | 0.29 | 0.48 | 0.28 | 0.24 | 0.13 | 0.13 | 0.14 | 0.15 |
| P11/P12 | 0.40 | 0.19 | 0.17 | 0.09 | 0.06 | 0.19 | 0.19 | 0.26 | 0.15 | 0.08 | $0.00^{NS}$ | -0.06 | 0.17 |
| P13/P14 | 0.52 | 0.39 | 0.39 | -0.02 | 0.04 | -0.06 | -0.04 | 0.36 | 0.39 | 0.08 | -0.02 | 0.12 | 0.12 |
| P2/P15 | 0.31 | 0.20 | 0.24 | 0.04 | -0.10 | 0.12 | $0.01^{NS}$ | 0.17 | 0.23 | 0.20 | 0.12 | 0.13 | 0.21 |
| P16/P13 | 0.40 | 0.28 | 0.25 | 0.16 | 0.08 | $0.00^{NS}$ | 0.24 | 0.20 | 0.30 | 0.26 | 0.22 | 0.17 | 0.25 |
| P17/P18 | 0.47 | 0.31 | 0.26 | -0.03 | 0.03 | 0.13 | 0.20 | 0.29 | 0.20 | 0.18 | 0.08 | 0.08 | 0.10 |
| P19/P20 | 0.22 | 0.09 | 0.24 | 0.35 | 0.09 | $0.00^{NS}$ | 0.21 | 0.16 | 0.15 | 0.16 | 0.10 | 0.04 | 0.19 |
| P21/P22 | 0.47 | 0.33 | 0.28 | 0.37 | 0.19 | 0.28 | 0.34 | 0.31 | 0.16 | 0.08 | 0.19 | 0.04 | 0.09 |
| P23/P24 | 0.20 | 0.09 | 0.04 | 0.38 | 0.12 | 0.13 | 0.30 | 0.07 | 0.02 | 0.02 | 0.05 | $0.00^{NS}$ | 0.06 |
| P25/P22 | 0.43 | 0.26 | 0.16 | 0.32 | 0.06 | 0.17 | 0.19 | 0.28 | 0.16 | 0.22 | 0.21 | 0.10 | 0.19 |
| P26/P27 | 0.24 | 0.13 | 0.17 | 0.07 | 0.09 | 0.03 | 0.12 | 0.12 | 0.15 | 0.22 | 0.18 | 0.12 | 0.27 |
| P23/P25 | 0.57 | 0.33 | 0.16 | 0.23 | 0.42 | 0.04 | 0.15 | 0.38 | 0.22 | 0.14 | 0.23 | 0.07 | 0.09 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P24/P26 | 0.47 | 0.35 | 0.06 | 0.05 | 0.05 | -0.05 | 0.02 | 0.29 | 0.05 | 0.06 | -0.06 | 0.02 | 0.04 |
| P28/P27 | 0.35 | 0.20 | -0.05 | 0.11 | 0.27 | 0.13 | 0.15 | 0.22 | 0.12 | 0.13 | 0.21 | 0.08 | 0.10 |
| P29/P27 | 0.25 | 0.15 | 0.02 | 0.12 | 0.06 | 0.03 | 0.08 | 0.11 | 0.03 | 0.08 | 0.10 | 0.01 | 0.06 |
| P29/P30 | 0.23 | 0.18 | 0.05 | 0.22 | 0.16 | 0.04 | 0.12 | 0.15 | 0.07 | 0.15 | 0.13 | 0.02 | 0.01$^{NS}$ |
| P31/P32 | 0.23 | 0.03 | 0.04 | 0.25 | 0.17 | 0.06 | -0.01$^{NS}$ | 0.05 | -0.01$^{NS}$ | 0.10 | 0.06 | 0.00$^{NS}$ | 0.04 |
| P33/P34 | 0.45 | 0.19 | -0.11 | -0.05 | 0.12 | -0.08 | -0.11 | 0.33 | 0.09 | 0.04 | 0.02 | 0.06 | 0.02 |
| P35/P36 | 0.27 | 0.16 | -0.15 | 0.00$^{NS}$ | 0.02 | -0.08 | -0.01$^{NS}$ | 0.17 | -0.60 | 0.04 | 0.06 | -0.09 | -0.01$^{NS}$ |
| P37/P38 | 0.29 | 0.25 | 0.43 | 0.06 | 0.11 | -0.17 | 0.50 | 0.27 | 0.24 | 0.07 | 0.03 | 0.01 | 0.08 |
| P39/P40/P39 | 0.46 | 0.13 | 0.02 | 0.20 | 0.09 | -0.02 | 0.03 | 0.18 | 0.06 | 0.11 | 0.09 | -0.13 | -0.05 |
| P41/P42 | 0.24 | 0.30 | 0.04 | 0.28 | 0.29 | -0.07 | -0.01$^{NS}$ | 0.27 | 0.12 | 0.18 | 0.15 | 0.00$^{NS}$ | 0.01$^{NS}$ |

†Heritability ($h^2$) on an entry-mean basis.

‡NS, not significantly different from zero (P=0.05). All other estimates of R and $r_{MP}$ were significant.

Table 4: Response to selection (R) and prediction accuracy ($r_{MP}$) for moisture with phenotypic selection (PS) and with the A/B, general combining ability (GCA), GCA-identity by descent ($GCA_{IBD}$), same background (SB), and SB+GCA models for genomewide selection in maize.

| Test population | $h^{2\dagger}$ | R (g kg$^{-1}$) | | | | | | $r_{MP}$ | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | PS | A/B | GCA | $GCA_{IBD}$ | SB | SB+GCA | PS | A/B | GCA | $GCA_{IBD}$ | SB | SB+GCA |
| P1/P2 | 0.58 | -6 | -5 | -5 | -5 | -2 | -4 | 0.35 | 0.37 | 0.46 | 0.46 | 0.29 | 0.29 |
| P3/P4 | 0.75 | -11 | -8 | -7 | -7 | -3 | -5 | 0.58 | 0.46 | 0.42 | 0.38 | 0.19 | 0.37 |
| P4/P5 | 0.76 | -6 | -5 | -4 | -4 | -3 | -4 | 0.51 | 0.48 | 0.29 | 0.31 | -0.01 | 0.38 |
| P6/P7 | 0.85 | -14 | -12 | -9 | -8 | -3 | -6 | 0.67 | 0.37 | 0.46 | 0.40 | 0.11 | 0.42 |
| P3/P8 | 0.73 | -6 | -6 | -7 | -6 | -2 | -5 | 0.46 | 0.41 | 0.38 | 0.36 | 0.11 | 0.36 |
| P1/ P9 | 0.55 | -2 | -3 | -3 | -4 | -2 | -4 | 0.26 | 0.26 | 0.30 | 0.25 | 0.17 | 0.34 |
| P5/P8 | 0.77 | -2 | -3 | -1 | -1 | 1 | -4 | 0.25 | 0.36 | 0.18 | 0.15 | 0.06 | 0.26 |
| P9/P10 | 0.56 | -15 | -11 | -13 | -6 | 2 | -2 | 0.61 | 0.47 | 0.28 | 0.16 | 0.06 | 0.17 |
| P9/P2/P9 | 0.75 | -4 | -4 | -3 | -2 | -1 | -4 | 0.43 | 0.39 | 0.35 | 0.26 | 0.21 | 0.38 |
| P11/P12 | 0.84 | -10 | -9 | -5 | -5 | -2 | -4 | 0.66 | 0.57 | 0.25 | 0.19 | 0.03 | 0.07 |
| P13/P14 | 0.68 | -2 | -2 | -2 | -2 | -2 | -4 | 0.38 | 0.36 | 0.23 | 0.21 | 0.20 | 0.19 |
| P2/P15 | 0.61 | -3 | -4 | -4 | -4 | -3 | -3 | 0.30 | 0.31 | 0.32 | 0.32 | 0.22 | 0.29 |
| P16/P13 | 0.76 | -8 | -10 | -8 | -8 | -1 | -5 | 0.56 | 0.58 | 0.53 | 0.48 | 0.14 | 0.49 |
| P17/P18 | 0.81 | -14 | -16 | -6 | -7 | -4 | -6 | 0.50 | 0.67 | 0.30 | 0.26 | 0.15 | 0.16 |
| P19/P20 | 0.56 | -6 | -3 | -3 | 1 | 1 | -2 | 0.39 | 0.22 | 0.16 | $-0.01^{NS\ddagger}$ | $0.00^{NS}$ | 0.11 |
| P21/P22 | 0.43 | -5 | -7 | -7 | -5 | -4 | -7 | 0.29 | 0.38 | 0.36 | 0.35 | 0.24 | 0.29 |
| P23/P24 | 0.62 | -7 | -5 | -4 | -4 | -1 | -2 | 0.40 | 0.34 | 0.29 | 0.23 | 0.21 | 0.30 |
| P25/P22 | 0.64 | -9 | -6 | -7 | -5 | -3 | -4 | 0.46 | 0.36 | 0.28 | 0.25 | 0.12 | 0.19 |
| P26/P27 | 0.74 | -8 | -6 | -6 | -4 | -2 | -4 | 0.53 | 0.48 | 0.42 | 0.32 | 0.17 | 0.19 |
| P23/P25 | 0.62 | -6 | -5 | -7 | -5 | -1 | -4 | 0.48 | 0.35 | 0.41 | 0.39 | 0.17 | 0.33 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P24/P26 | 0.71 | -7 | -6 | -7 | -1 | 0[NS] | -6 | 0.50 | 0.38 | 0.40 | -0.02 | 0.04 | 0.31 |
| P28/P27 | 0.81 | -13 | -11 | -8 | -9 | -4 | -8 | 0.62 | 0.56 | 0.43 | 0.51 | 0.13 | 0.29 |
| P29/P27 | 0.75 | -6 | -5 | -5 | -4 | -3 | -4 | 0.52 | 0.49 | 0.49 | 0.38 | 0.20 | 0.41 |
| P29/P30 | 0.63 | -5 | -4 | -4 | -4 | 1 | -2 | 0.45 | 0.44 | 0.36 | 0.34 | 0.03 | 0.30 |
| P31/P32 | 0.42 | -6 | -6 | -5 | -5 | 0[NS] | -3 | 0.40 | 0.26 | 0.24 | 0.20 | 0.01[NS] | 0.21 |
| P33/P34 | 0.51 | -9 | -4 | -6 | -5 | -1 | -5 | 0.35 | 0.12 | 0.20 | 0.15 | 0.04 | 0.14 |
| P35/P36 | 0.59 | -3 | 1 | 0[NS] | 0[NS] | 1 | 0[NS] | 0.29 | 0.05 | -0.02 | 0.05 | -0.01 | -0.02 |
| P37/P38 | 0.38 | -7 | -6 | -6 | -3 | 4 | -2 | 0.40 | 0.24 | 0.24 | 0.15 | -0.07 | 0.22 |
| P39/P40/P39 | 0.61 | -2 | -2 | -2 | 0[NS] | 1 | -1 | 0.21 | 0.24 | 0.15 | -0.01 | 0.04 | 0.03 |
| P41/P42 | 0.73 | -10 | -9 | -11 | -8 | -2 | -3 | 0.53 | 0.55 | 0.40 | 0.33 | 0.09 | 0.09 |

[†]Heritability ($h^2$) on an entry-mean basis.

[‡]NS, not significantly different from zero (P=0.05). All other estimates of R and $r_{MP}$ were significant.

Table 5: Response to selection (R) and prediction accuracy ($r_{MP}$) for test weight with phenotypic selection (PS) and with the A/B, general combining ability (GCA), GCA-identity by descent ($GCA_{IBD}$), same background (SB), and SB+GCA models for genomewide selection in maize.

| Test population | $h^{2\dagger}$ | R (kg $hL^{-1}$) | | | | | | $r_{MP}$ | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | PS | A/B | GCA | $GCA_{IBD}$ | SB | SB+GCA | PS | A/B | GCA | $GCA_{IBD}$ | SB | SB+GCA |
| P1/P2 | 0.32 | 0.39 | 0.25 | 0.32 | 0.37 | 0.45 | 0.40 | 0.22 | 0.22 | 0.37 | 0.38 | 0.35 | 0.33 |
| P3/P4 | 0.52 | 0.63 | 0.34 | 0.19 | 0.10 | -0.02 | 0.12 | 0.32 | 0.25 | 0.12 | 0.10 | $-0.01^{NS\ddagger}$ | 0.06 |
| P4/P5 | 0.31 | 0.40 | 0.14 | 0.47 | 0.20 | 0.13 | 0.67 | 0.16 | 0.09 | 0.22 | 0.16 | -0.07 | 0.12 |
| P6/P7 | 0.83 | 1.06 | 0.75 | 0.50 | 0.74 | 0.04 | 0.38 | 0.62 | 0.11 | 0.33 | 0.30 | 0.03 | 0.28 |
| P3/P8 | 0.67 | 0.72 | 0.63 | 0.11 | 0.09 | 0.07 | 0.11 | 0.44 | 0.45 | 0.31 | 0.29 | 0.10 | 0.21 |
| P1/ P9 | 0.47 | 0.46 | 0.16 | 0.26 | 0.23 | 0.29 | 0.31 | 0.24 | 0.16 | 0.24 | 0.14 | 0.07 | 0.18 |
| P5/P8 | 0.47 | 0.58 | 0.37 | 0.63 | 0.42 | -0.26 | 0.21 | 0.32 | 0.28 | 0.28 | 0.21 | -0.02 | 0.26 |
| P9/P10 | 0.52 | 0.73 | 0.39 | 0.69 | 0.14 | -0.15 | 0.46 | 0.35 | 0.29 | 0.36 | 0.23 | $0.00^{NS}$ | 0.21 |
| P9/P2/P9 | 0.46 | 0.39 | 0.47 | 0.24 | 0.41 | -0.22 | 0.20 | 0.24 | 0.19 | 0.19 | 0.17 | -0.01 | 0.17 |
| P11/P12 | 0.52 | 0.42 | 0.29 | 0.23 | 0.13 | 0.20 | 0.21 | 0.28 | 0.26 | 0.12 | 0.11 | 0.08 | 0.16 |
| P13/P14 | 0.62 | 0.25 | 0.32 | 0.27 | 0.22 | 0.20 | 0.20 | 0.32 | 0.27 | 0.20 | 0.22 | 0.02 | 0.13 |
| P2/P15 | 0.35 | 0.27 | 0.09 | 0.14 | 0.25 | 0.05 | 0.13 | 0.10 | 0.06 | 0.16 | 0.18 | 0.12 | 0.15 |
| P16/P13 | 0.71 | 0.67 | 0.78 | 0.71 | 0.38 | 0.08 | 0.50 | 0.48 | 0.60 | 0.43 | 0.35 | -0.03 | 0.32 |
| P17/P18 | 0.71 | 0.62 | 0.83 | -0.06 | -0.07 | -0.31 | -0.31 | 0.50 | 0.51 | -0.05 | 0.03 | -0.05 | -0.07 |
| P19/P20 | 0.66 | 0.79 | 0.50 | 0.19 | 0.11 | 0.01 | 0.20 | 0.38 | 0.18 | 0.04 | 0.09 | 0.05 | 0.07 |
| P21/P22 | 0.54 | 0.68 | 0.46 | 0.87 | 0.27 | -0.06 | 0.91 | 0.33 | 0.33 | 0.33 | 0.25 | 0.05 | 0.33 |
| P23/P24 | 0.45 | 0.56 | 0.30 | 0.15 | 0.14 | 0.04 | 0.19 | 0.31 | 0.23 | 0.19 | 0.07 | 0.11 | 0.15 |
| P25/P22 | 0.61 | 0.57 | 0.31 | 0.34 | 0.49 | $0.01^{NS}$ | 0.37 | 0.42 | 0.25 | 0.27 | 0.27 | 0.10 | 0.22 |
| P26/P27 | 0.69 | 0.73 | 0.85 | 0.76 | 0.49 | 0.75 | 0.80 | 0.51 | 0.55 | 0.48 | 0.39 | 0.16 | 0.18 |
| P23/P25 | 0.51 | 0.75 | 0.68 | 0.48 | 0.64 | 0.56 | 0.45 | 0.35 | 0.36 | 0.24 | 0.30 | 0.12 | 0.22 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P24/P26 | 0.72 | 0.85 | 0.69 | 0.68 | -0.21 | 0.45 | 0.07 | 0.52 | 0.49 | 0.42 | -0.06 | 0.30 | -0.23 |
| P28/P27 | 0.46 | 0.43 | 0.17 | 0.17 | 0.12 | 0.01$^{NS}$ | 0.02 | 0.27 | 0.18 | 0.13 | -0.07 | -0.01 | 0.02 |
| P29/P27 | 0.60 | 0.55 | 0.51 | 0.49 | 0.28 | 0.28 | 0.44 | 0.41 | 0.43 | 0.41 | 0.28 | 0.23 | 0.34 |
| P29/P30 | 0.28 | 0.04 | 0.06 | 0.33 | 0.19 | -0.10 | 0.27 | 0.07 | 0.14 | 0.31 | 0.28 | 0.00$^{NS}$ | 0.25 |
| P31/P32 | 0.45 | 0.40 | 0.68 | 0.67 | 0.09 | -0.29 | 0.46 | 0.27 | 0.32 | 0.28 | 0.13 | -0.03 | 0.24 |
| P33/P34 | 0.59 | 0.81 | 0.38 | 0.29 | 0.50 | 0.59 | 0.25 | 0.43 | 0.32 | 0.22 | 0.16 | 0.11 | 0.20 |
| P35/P36 | 0.27 | 0.36 | 0.10 | -0.02 | -0.30 | 0.28 | 0.15 | 0.17 | 0.06 | -0.02 | 0.01 | 0.07 | 0.05 |
| P37/P38 | 0.38 | 0.41 | 0.73 | 0.73 | 0.39 | 0.00$^{NS}$ | 0.12 | 0.49 | 0.55 | 0.39 | 0.28 | 0.17 | 0.36 |
| P39/P40/P39 | 0.62 | 0.42 | 0.34 | 0.13 | 0.25 | 0.19 | 0.34 | 0.17 | 0.25 | 0.08 | 0.18 | 0.09 | 0.20 |
| P41/P42 | 0.7 | 0.73 | 0.65 | 0.41 | 0.19 | 0.18 | 0.20 | 0.55 | 0.37 | 0.17 | 0.12 | 0.01$^{NS}$ | 0.04 |

†Heritability ($h^2$) on an entry-mean basis.

‡NS, not significantly different from zero (P=0.05). All other estimates of R and $r_{MP}$ were significant.

Table 6: Correlation between prediction accuracy ($r_{MP}$) versus the number of individuals in the training population ($N_{GCA}$), number of biparental crosses in the training population ($N_X$), heritability ($h^2$), linkage disequilibrium ($r^2$), and number of markers ($N_M$).

| Factor | Grain yield | Moisture | Test weight |
|---|---|---|---|
| $N_{GCA}$[†] | 0.18 | 0.43* | 0.33 |
| $N_X$[‡] | 0.13 | 0.42* | 0.38* |
| $h^2$[§] | 0.16 | 0.39* | 0.14 |
| $r^2$[¶] | 0.29 | 0.35 | 0.15 |
| $h^2\sqrt{N_{GCA}}$ | 0.26 | 0.57* | 0.43* |
| $h^2r^2\sqrt{N_{GCA}}$ | 0.36* | 0.58* | 0.48* |
| $h^2\sqrt{N_X}$ | 0.22 | 0.55* | 0.46* |
| $h^2r^2\sqrt{N_X}$ | 0.31 | 0.57* | 0.52* |
| $N_M$[#] | 0.35 | 0.01 | 0.18 |

[†]$N_{GCA}$, number of individuals in the training population for the GCA model.

[‡]$N_X$, number of biparental crosses in the training population for the GCA model.

[§]$h^2$, heritability on an entry-mean basis.

[¶]$r^2$, mean LD between adjacent SNP markers.

[#]$N_M$, number of markers.

*Significant ($P$ = 0.05) based on a Fisher z-transformation. All other correlation coefficients were nonsignificant.

## Chapter 2: Marker imputation prior to genomewide selection in biparental maize populations

Marker imputation increases the number of markers in genomewide selection. Our objectives were to determine: (i) if marker imputation increases the response to selection (R) and prediction accuracy ($r_{MP}$) among the progeny of two maize (*Zea mays* L.) parental inbreds (A and B); (ii) the number of imputed single nucleotide polymorphism (SNP) markers needed to reach a plateau in $r_{MP}$ for grain yield, moisture, and test weight; and (iii) the lowest number of assayed SNP markers that can be used for imputation without a significant decrease in $r_{MP}$. The progeny of 27 A/B crosses were assayed with 49 to 100 SNP markers, and imputation was conducted to increase the number of markers to 2911. For each A/B test population, the training population in the general combining ability (GCA) model consisted of 4 to 26 maize crosses with A and B as one of the parents, whereas the training population in the A/B model was the A/B population itself. Marker imputation made the GCA model as good as or better than the A/B model in terms of R and $r_{MP}$ for all the traits. The $r_{MP}$ values did not increase significantly beyond 500 imputed markers for grain yield, and beyond 1000 imputed markers for moisture and test weight. We recommend that maize breeders should assay a biparental cross with only around 50 polymorphic SNP markers, increase marker coverage to around 1000 markers by imputation, and use the GCA model with imputed markers for genomewide selection within a biparental cross.

## Introduction

Maize (*Zea mays* L.) breeding has traditionally involved developing lines from the cross between two inbreds, and evaluating the lines for their field performance when crossed with an inbred tester (Hallauer, 1990). In a previous study, we found that a general combining ability (GCA) model is useful for genomewide selection among progeny within a biparental cross (Jacobson et al., 2014). Suppose inbreds A and B are the parents of a biparental cross, and * is any inbred that belongs to the same heterotic group as A and B. In the GCA model, multiple A/* and */B populations that have previously been evaluated are used as a training population to predict the testcross performance of progeny in the A/B test population. We found that for grain yield, moisture, and test weight in 30 A/B maize populations, the responses (denoted by R) to genomewide selection with the GCA model were 68 to 76% of the corresponding R values with phenotypic selection (Jacobson et al., 2014). Because the GCA model relies on A/* and */B populations that have been previously phenotyped and genotyped, it eliminates the need to phenotype any of the progeny in the A/B population itself. On average, genomewide selection with the GCA model increased maize grain yield by 0.19 Mg ha$^{-1}$ prior to any phenotyping of the A/B cross itself (Jacobson et al., 2014).

The number of markers (denoted by $N_M$) used in genomewide selection affects its accuracy, which is measured as the correlation between the marker-predicted values and phenotypic values ($r_{MP}$) (Lorenzana and Bernardo, 2009; Heffner et al., 2011a; Combs and Bernardo, 2013a). In each of the 30 A/B populations in our previous study (Jacobson et al., 2014), $N_M$ ranged from 49 to 100 single nucleotide polymorphism (SNP) markers, and the mean linkage disequilibrium between adjacent markers ranged from $r^2$ = 0.36 to 0.64. A

larger $N_M$ may lead to higher linkage disequilibrium between the SNP markers and the underlying quantitative trait loci (QTL) (Servin and Stephens, 2007; Guan and Stephens, 2008; Iwata and Jannink, 2010). In turn, a higher linkage disequilibrium may lead to a higher $r_{MP}$ (Lian et al., 2014) and a larger R. On the other hand, a larger $N_M$ may increase the cost of genomewide selection.

Marker imputation, which is the prediction of missing SNP data on the basis of information on nearby SNP markers, can be used to effectively increase $N_M$ in a cost-effective way (Scheet and Stephens, 2006; Marchini et al., 2007; Purcell et al., 2007; Browning and Browning, 2007; Hickey et al., 2012). Whereas the A/B, A/*, and */B populations in our study (Jacobson et al., 2014) were genotyped at 100 or fewer SNP markers, the parents of the populations were genotyped at 2911 SNP loci. By imputation, the marker genotypes of all of the lines can be predicted for the ~2800 SNP markers that were not assayed in the test (A/B) and training populations (A/* and */B). Marker imputation is therefore performed for both the training population and test population. Further reductions in the cost of genotyping will result if the GCA model, coupled with marker imputation from parental data, is found effective even with very few markers (30 to 50 SNPs) assayed in the training and test populations.

The usefulness of marker imputation in the GCA model for a biparental cross has not been studied. Therefore, our objectives in this study were to determine: (i) if marker imputation increases R and $r_{MP}$ within maize biparental crosses; (ii) the $N_M$ needed to reach a plateau in $r_{MP}$ for grain yield, moisture, and test weight in maize biparental crosses; and (iii) the lowest number of assayed SNP markers that can be used for imputation without a significant decrease in $r_{MP}$.

## Materials and Methods

### *Test and Training Populations*

Phenotypic and marker data for 969 biparental testcross populations were provided to us by Monsanto. The populations used in this study were the same populations used by Jacobson et al. (2014) and Lian et al. (2014), except that only the $F_2$ populations (which were represented by $F_3$ lines) were used in the current study. A total of 27 A/B test populations were selected based on having at least four A/* and */B populations, a minimum population size of 50 $F_3$ lines, and an entry-mean heritability ($h^2$) significantly greater than zero. The A/B, A/*, and */B populations were all crossed to the same inbred tester, and all of the phenotypic data were for testcrosses.

The testcrosses of the $F_3$ lines were evaluated for grain yield (Mg $ha^{-1}$), moisture (g $kg^{-1}$), and test weight (kg $hL^{-1}$) at 4 to 12 environments in the United States from 2001 to 2008. Testcross genetic ($V_G$) and nongenetic ($V_R$) variance components were calculated by restricted maximum likelihood using the lme4 package (Bates et al., 2013) in R statistical software (Holland et al., 2003; R Development Core Team, 2012). The genotype by environment interaction variance and the within-location error variance were confounded in $V_R$ due to the phenotypic data available as the testcross mean of each $F_3$ line within each location. A likelihood ratio test was used to determine the significance of the estimates of $V_G$. The p-value of the likelihood ratio test was divided by 2.0 to approximate an F-test of the null hypothesis, and a p-value $<0.05$ was considered significant (Holland et al., 2003). The data for each cross were not completely balanced because some testcrosses were not evaluated in all of the locations in each experiment. The $h^2$ was then estimated on an ad

hoc basis as $h^2 = V_G/(V_G + V_R/e)$, where $e$ was the harmonic mean of the number of locations (Holland et al., 2003).

*Markers Imputation*

The parents of the A/B, A/*, and */B populations were genotyped with 2911 SNP markers, whereas the progeny in each cross were genotyped at a low density with 49 to 100 SNP markers polymorphic between A and B. The genotypes at each marker locus were coded as 1 if the $F_3$ line was homozygous for the SNP allele from parent A, –1 if the $F_3$ line was homozygous for the SNP from parent B, and 0 if the $F_3$ line was heterozygous. As described in the next paragraph, we imputed the markers from the progeny coverage of 49–100 SNP markers to the parental marker coverage of 2911 SNP markers.

The observed linkage disequilibrium was calculated as the mean $r^2$ value between adjacent SNP markers with R statistical software (R Development Core Team, 2012). A proprietary consensus linkage map was provided by Monsanto. The total length of the consensus map was 1852 cM, with the 10 linkage groups ranging from 123 to 257 cM. The number of markers per chromosome ranged from 191 to 463. The expected linkage disequilibrium between two markers in the $F_2$ of a biparental cross was calculated as $r^2 = (1 - 2c)^2$ (Lian et al., 2014), where $c$ was the mean recombination rate between a pair of markers for a given marker density. The Kosambi mapping function was used to obtain the value of $c$ from the mean cM distance between adjacent markers.

Marker imputation was performed on the basis of the conditional probabilities of marker genotypes, given the estimated recombination rates with the nearest non-missing flanking markers. The conditional probabilities were obtained by dividing the joint probabilities found in Table 10.5 in Wu et al. (2007) by the marginal probabilities. Suppose

the left flanking marker is A, the right flanking marker is B, and their recombination frequency is *c*. The marginal probability was $(1 - c)^2/4$ for AABB and aabb; $c(1 - c)/2$ for AABb, aaBb, AaBB, and Aabb; $c^2/4$ for AAbb and aaBB; and $[(1 - c)^2 + c^2]/2$ for AaBb. If the flanking marker was also missing, the next available flanking marker was used. The recombination rates were estimated from the consensus linkage map through the Kosambi mapping function. The marker genotypes were imputed one at a time along the chromosome. The probability of each marker genotype (coded as 1, 0, or –1) was calculated and the marker genotype with the highest probability was chosen. Preliminary analysis indicated the use of marker incidence matrices with the highest-probability genotypes (1, 0, or –1) instead of with the actual probabilities (e.g., 0.2, 0.6, –0.2) did not affect the results regarding the usefulness of marker imputation (results not shown). We wrote all code for imputation in R statistical software (R Development Core Team, 2012).

Software packages available for marker imputation include fastPHASE (Scheet and Stephens, 2006), BEAGLE (Browning and Browning, 2007), IMPUTE (Marchini et al., 2007) and PLINK (Purcell et al., 2007). The methods used in these software packages rely on localized patterns of linkage disequilibrium. In contrast, the conditional probabilities of marker genotypes are known in the $F_2$ of a cross between two parental inbreds. We therefore chose to rely on the known expected probabilities of marker genotypes in an $F_2$, rather than on the use of general approaches for imputing marker genotypes in populations or germplasm collections that do not have a well-defined structure.

*A/B and A/B$_I$ Models*

We first studied the influence of marker imputation on the A/B model, which involved a subset of $F_3$ lines from the A/B population as the training population and the

remaining $F_3$ lines as the test population (Jacobson et al., 2014). We compared an A/B model that utilized only the SNP markers that were assayed in the A/B, A/*, and */B crosses, versus an A/B model (denoted by $A/B_I$) that utilized marker imputation to increase $N_M$ to 2911.

For both the A/B and $A/B_I$ models, the values of R and $r_{MP}$ were calculated by a delete-one procedure along with cross-validation across environments as described by Jacobson et al. (2014). Marker effects were estimated by ridge regression-best linear unbiased prediction (RR-BLUP) using the package rrBLUP version 4.0 in R statistical software (Piepho, 2009; Endelman, 2011; R Development Core Team, 2012). With $N$ $F_3$ lines in an A/B cross, the performance of the first $F_3$ line was predicted from RR-BLUP analysis of the marker effects among the remaining $N - 1$ $F_3$ lines. For each trait, the performance of the first $F_3$ line was predicted as $y_P = \mu + \mathbf{Xm}$, where $y_P$ was the predicted performance of the $F_3$ line; $\mu$ was the estimated mean of the $N - 1$ $F_3$ lines used as the training population; $\mathbf{X}$ was a $1 \times N_M$ row vector of genotype indicators; and $\mathbf{m}$ was an $N_M \times 1$ vector of RR-BLUP marker effects, estimated from the remaining $N - 1$ $F_3$ lines. This delete-one analysis was repeated for all of the remaining $N - 1$ $F_3$ lines.

In addition to the delete-one analysis, cross-validation was also conducted across environments to eliminate a bias present in the A/B model due to the test and training populations being evaluated in the same environments (Jacobson et al., 2014). The RR-BLUP marker effects were estimated from the performance of the $N - 1$ $F_3$ lines in half of the environments and the marker effects were used to predict the performance of the test $F_3$ lines in the remaining half of the environments. Cross-validation was done for all combinations of environments.

Selection was for high grain yield, low moisture, and high test weight. The values of R were calculated from the mean of the top 10% of $F_3$ lines with the best $y_P$ values for each trait. The mean performance of the best $F_3$ lines in the other half of the environments was denoted $y_{0.10}$. The R values were obtained as $y_{0.10} - \mu$. The variances of R and $r_{MP}$ were obtained across the cross-validation repeats. These variances were used to calculate the LSD values ($P = 0.05$) for the mean $r_{MP}$ and mean R.

*General Combining Ability Model*

All available A/* $F_2$ populations (with $F_3$ lines) and */B $F_2$ populations (with $F_3$ lines) were used as the training population for the A/B cross. As previously mentioned, the A/B, A/*, and */B populations were crossed to same tester. The number of A/* and */B populations pooled in the training population ($N_X$) ranged from 4 to 26, and the total number of $F_3$ lines in the training population ($N_{GCA}$) ranged from 524 to 4357 (Table 7). We studied three variations of the GCA model: one that did not involve marker imputation (referred to as the GCA model), and two that involved marker imputation (referred to as the $GCA_I$ and $GCA_P$ models).

In the GCA model (Jacobson et al., 2014), different sets of SNP markers were used in each population, making it necessary to analyze each A/* and */B cross separately to obtain the RR-BLUP marker effects within each cross. For a given trait, the performance of all $N$ $F_3$ lines in the A/B test population was predicted as $\mathbf{y} = \mu\mathbf{1} + \mathbf{Xm}$, where $\mathbf{y}$ was an $N \times 1$ vector of predicted performance; $\mu$ was the estimated overall mean; $\mathbf{1}$ was an $N \times 1$ vector with elements equal to 1; $\mathbf{X}$ was an $N \times N_M$ matrix of genotype indicators with elements of 1, –1, and 0; and $\mathbf{m}$ was an $N_M \times 1$ vector of RR-BLUP marker effects averaged across the A/* and */B crosses. Markers in the A/B test population were disregarded if they

were not present in at least two A/* and */B crosses. Cross-validation across environments was done for the A/B test population according to the same procedure for splitting environments used in the A/B model. However, data from all environments were always used in estimating marker effects within the A/* and */B populations, which were evaluated in sets of environments different from those used to evaluate the A/B cross.

In the $GCA_I$ model, the data on all $N_M$ = 2911 SNP markers (which included the assayed markers and imputed markers) were used in the RR-BLUP analysis. Marker effects were estimated separately within each A/* and */B population and were averaged across the A/* and */B training populations. Cross-validation was conducted as described for the GCA model.

In the $GCA_P$ model, marker effects were likewise obtained for all $N_M$ = 2911 markers. But unlike in the $GCA_I$ model, in which the A/* and /*B population were analyzed separately, the $GCA_P$ model involved pooling all of the $F_3$ lines in the A/* and */B populations into one training population and conducting a single RR-BLUP analysis. For a given trait, the performance of the $N$ $F_3$ lines in the A/B test population was predicted as $\mathbf{y} = \mathbf{Zb} + \mathbf{Xm}$, where $\mathbf{y}$ was an $N \times 1$ vector of predicted performance; $\mathbf{b}$ was an $N_X \times 1$ vector of fixed effects of populations; $\mathbf{Z}$ was an $N \times N_X$ incidence matrix that related $\mathbf{y}$ to $\mathbf{b}$; $\mathbf{X}$ was an $N \times 2911$ matrix of genotype indicators with elements of 1, –1, and 0; and $\mathbf{m}$ was an $2911 \times 1$ vector of RR-BLUP marker effects.

*Phenotypic Selection*

In phenotypic selection within an A/B population, the mean performance of the $N$ $F_3$ lines in half of the environments was considered the predictor of the performance of the same lines in the remaining half of the environments. The prediction accuracy and R were

calculated the same as in the A/B model. For convenience, the prediction accuracy of phenotypic selection was also denoted by $r_{MP}$ even though the prediction of the performance did not involve marker effects.

*Reduced Marker Sets*

We evaluated R and $r_{MP}$ when the total number of markers used in genomewide selection was less than the full set of 2911 SNP markers. We chose a subset of $N_{M(Sub)}$ = 250, 500, 1000 and 2000 markers for RR-BLUP analysis. The same subset of $N_{M(Sub)}$ markers was used for all 27 A/B test populations. Each subset of $N_{M(Sub)}$ markers was chosen according to a five-step procedure that considered both marker spacing and minor allele frequency (Zhang and Druet, 2010). First, the number of markers per chromosome was calculated as $N_{M(Sub)}$ multiplied by the size of each chromosome, and divided by the size of the genome. Second, each chromosome was divided into bins. The size of each bin was equal to the size of the chromosome divided by the number of markers for that chromosome. Third, the marker (out of the original 2911 SNP loci) for the first bin on a given chromosome was chosen as the marker with the highest minor allele frequency. The allele frequencies were calculated from a set of 533 inbreds from the Monsanto breeding program; these inbreds included all of the parents of the A/B, A/*, and */B crosses used in this study. Fourth, the marker for the next bin was chosen based on the equation, $S_i = M_i(z - |z - d_i|)$, where $S_i$ was the score for the $i$th marker locus, $M_i$ was the minor allele frequency for the $i$th marker locus, $z$ was the size of the bin, and $d_i$ was the difference between the positions of the marker locus chosen for the previous bin and the $i$th marker locus. The marker locus (out of the original 2911 SNP loci) with the highest $S_i$ score within the bin

was chosen. Fifth, the above procedures were repeated for the remaining bins along the chromosome and for other chromosomes.

The markers assayed in each population were combined with the subset of $N_{M(Sub)}$ markers. Consequently, the final number of markers varied slightly for each population. Consider the set of $N_{M(Sub)}$ = 1000 markers. The P1/P2 cross was assayed with 79 markers (Table 7), and 11 out of these 79 assayed markers were part of the $N_{M(Sub)}$ = 1000 markers. For $N_{M(Sub)}$ = 1000, the final number of markers used in the P1/P2 cross was therefore 1000 + 79 – 11 = 1068. The P3/P4 cross was assayed with 58 markers, 6 of which were part of the $N_{M(Sub)}$ = 1000 markers. For $N_{M(Sub)}$ = 1000, the final number of markers used in the P3/P4 cross was therefore 1000 + 58 – 6 = 1052. For convenience, we refer to the comparison as $N_{M(Sub)}$ = 1000 despite the slight differences in the numbers of markers used.

The procedures previously described for the GCA model with 2911 SNP markers were then conducted for each set of $N_{M(Sub)}$ = 250, 500, 1000 and 2000 markers. In addition, we determined whether the GCA model is effective if only 30, 40, and 50 SNP markers are assayed per population, but marker imputation is then used to effectively increase $N_M$. From the SNP markers that were assayed in each A/B, A/* and */B population, we chose subsets of 30, 40, and 50 SNP markers according to the procedure described in the previous paragraph. On the basis of the genotypes at the 30, 40, and 50 marker subsets, imputation was performed to obtain data for the $N_{M(Sub)}$ = 500 and 1000 subsets of markers referred to in the previous paragraph. The imputed marker datasets were subsequently used in the GCA model.

## Results and Discussion

*Genomewide Selection without Imputation*

When marker imputation was not done, the overall ranking of the models for R and $r_{MP}$ among the 27 A/B maize populations was as follows: phenotypic selection > A/B model > GCA model (Table 8). The ranking of these three models was the same for grain yield, moisture, and test weight. Across all three traits, the A/B model led to R values that were 68 to 74% of the R values with phenotypic selection. The GCA model led to R values that were 59 to 64% of the R values with phenotypic selection. The results in Table 8 are slightly different from those we previously reported (Jacobson et al., 2014) because our previous study included 27 $F_2$ populations, and 2 backcross populations, whereas the current study included the 27 $F_2$ populations only.

*Genomewide Selection with Imputation*

In this study, the accuracy of imputation itself could not be measured because the A/B, A/*, and */B populations were not assayed with high density markers. The usefulness of marker imputation was therefore studied on the basis of the change in R and $r_{MP}$. Averaged across the 27 A/B populations, marker imputation with the A/B model did not lead to a significant ($P = 0.05$) increase in either R or $r_{MP}$ for any of the three traits (Table 8). However, the R and $r_{MP}$ within several populations was significantly higher with the $A/B_I$ model than with the A/B model. The number of populations with a significant increase in R due to imputation in the A/B model was four for grain yield, five for moisture, and two for test weight (Tables 9, 10 and 11). The number of populations with a significant increase in $r_{MP}$ due to imputation in the A/B model was six for grain yield, six for moisture,

and five for test weight (Tables 9, 10 and 11). The populations with the largest increase in R and $r_{MP}$ were those assayed with the fewest markers. For example, population P28/P27 was assayed with 49 markers, and R increased from –0.05 to 0.08 Mg ha$^{-1}$ for grain yield, –11 to –13 g kg$^{-1}$ for moisture, and 0.14 to 0.29 kg hL$^{-1}$ for test weight. Overall, however, imputation did not lead to a significant improvement of the A/B model (Table 8).

In contrast, marker imputation led to an overall improvement of the GCA model. The mean $r_{MP}$ was significantly higher with the $GCA_I$ and $GCA_P$ models than with the GCA model (Table 8). The increase in $r_{MP}$ due to the increase in $N_M$ is in agreement with previous studies (Bernardo and Yu, 2007; Lorenzana and Bernardo, 2009; Heffner et al., 2011a; Combs and Bernardo, 2013a). The R values for the GCA, $GCA_I$, and $GCA_P$ models were not significantly different for grain yield and for moisture, but the R values for test weight were significantly higher with the $GCA_I$ and $GCA_P$ models than with the GCA model (Table 8). The number of populations in which imputation caused a significant increase in $r_{MP}$ was 12 for grain yield, 15 for moisture, and 12 for test weight (Tables 9, 10 and 11), and the number of populations with a significant increase in R was 9 for grain yield, 7 for moisture and 13 for test weight (Tables 9, 10 and 11). Overall, the significant increase in mean $r_{MP}$ for all of the traits, and significant increase in mean R for test weight (Table 8) indicated that marker imputation is advantageous in the GCA model.

A benefit of imputation is that all of the A/B, A/*, and */B populations have data for the same set of SNP markers. In the $GCA_I$ model, RR-BLUP marker effects were calculated within each A/* and */B population and the marker effects were averaged to predict the performance of the A/B lines. In the $GCA_P$ model, all of the A/* and */B populations were pooled and the marker effects were estimated by RR-BLUP analysis of

the pooled $F_3$ lines. There were no significant differences in R and in $r_{MP}$ between the $GCA_I$ and $GCA_P$ models (Table 8). These results indicated that estimating marker effects within each A/* and */B population is as effective as pooling all of the A/* and */B populations and estimating the marker effects at once. Because the $GCA_I$ and $GCA_P$ models performed equally well, we describe the results for the less computationally intensive $GCA_I$ model in the rest of this article.

The overall ranking of the models changed from phenotypic selection > A/B > GCA without imputation, to phenotypic selection > $GCA_I$ > $A/B_I$ with imputation. The GCA model led to R values that were 59 to 64% of the R values with phenotypic selection, and the $GCA_I$ model led to R values that were 84 to 88% of the R values with phenotypic selection. Genomewide selection becomes more effective as the genetic similarity between the test population and the training population increases (Habier et al., 2010; Asoro et al., 2011; Clark et al., 2012) and as the size of the training population increases (Lorenzana and Bernardo, 2009; Daetwyler et al., 2010; Heffner et al., 2011a; Albrecht et al., 2011; Guo et al., 2012; Combs and Bernardo, 2013a). The genetic similarity between the test and training populations is higher in the A/B model than in the GCA model, whereas the training population is larger in the GCA model than in the A/B model. Our results indicated that marker imputation coupled with the larger training populations in the $GCA_I$ model can compensate for the lower genetic similarity between the test and training populations in the $GCA_I$ model. From a practical standpoint, the GCA model is preferable over the A/B model because it does not require phenotyping any of the progeny in the A/B population (Jacobson et al., 2014).

The improvement in R and $r_{MP}$ due to imputation was greater for the $GCA_I$ model than the $A/B_I$ model. We attribute this result to a lower linkage disequilibrium initially present (before imputation) in the training populations for GCA model than in the training populations for the A/B model. For the A/B model, the mean $r^2$ among the assayed markers was 0.43, and the mean $r^2$ among the imputed markers was 0.93. The mean $r^2$ among the assayed markers could not be determined for the GCA model because the A/* and */B populations were assayed with different sets of markers. However, the mean $r^2$ among the imputed markers was 0.49 in the pooled A/* and */B populations. This mean $r^2$ of 0.49 among 2911 SNP markers suggested that the mean $r^2$ among the 49 to 100 assayed markers (prior to imputation) was much lower than 0.49 in the GCA model. The potential for increasing linkage disequilibrium in the training population was therefore greater in the GCA model than in the A/B model, and this led to marker imputation being more useful in the GCA model than in the A/B model.

*Imputation to and from Different Numbers of Markers*

Linkage disequilibrium increased as the number of markers increased. Across the 27 A/B populations, the mean $r^2$ between adjacent markers was 0.48 for the markers assayed within each cross, 0.78 for 250 markers, 0.84 for 500 markers, 0.89 for 1000 markers, 0.92 for 2000 markers, and 0.93 for 2911 markers. We note that these mean $r^2$ values for 250 to 2911 markers were calculated from a mixture of non-imputed and imputed marker data. The expected linkage disequilibrium is theoretically derived by the equation $r^2 = (1-2c)^2$ (Lian et al., 2014), with c defined as the recombination rate derived from the Kosambi mapping function based on the mean cM distance between adjacent markers. Theoretically the $r^2$ values are then calculated to be 0.22 for the markers assayed

within each, 0.72 for 250 markers, 0.86 for 500 markers, 0.93 for 1000 markers, 0.96 for 2000 markers and 0.98 for 2911 markers. The expected and observed $r^2$ differed for the marker assayed within each cross for the original assayed markers. The expected $r^2$ was calculated based on even marker spacing but the assayed markers were not equally spaced along the chromosome and among chromosomes. The difference was more pronounced at the lower marker density but $r^2$ only slightly varied for the imputed marker datasets.

Linkage disequilibrium is highly correlated with prediction accuracy (Lian et al., 2014), and it contributed to the plateau in $r_{MP}$ when increasing numbers of markers were used. The mean $r_{MP}$ did not significantly increase beyond 500 imputed markers for grain yield, and beyond 1000 imputed markers for moisture and test weight (Fig. 1). Assuming evenly spaced markers in a 1852 cM genome, these numbers of markers are equivalent to having markers spaced 2 to 4 cM apart. In an intermated B73 × Mo17 population of 233 maize recombinant inbreds, the $r_{MP}$ in the A/B model did not increase consistently after marker density above one marker per 12.5 cM (Combs and Bernardo, 2013a). In a maize population of 371 doubled haploids, the prediction accuracy in the A/B model plateaued when the mean distance between markers approached 25 cM (Lorenzana and Bernardo, 2009). Simulations have shown that the increase in $N_M$ without an increase in $N$ does not necessarily improve the prediction accuracy (Muir, 2007). We speculate on two reasons for the optimum marker spacing being tighter (2 to 4 cM) in this study than in the Lorenzana and Bernardo (2009) and Combs and Bernardo (2013a). The first reason is that the training populations were larger in the current study (524 to 4357 lines, Table 7) than with these two previous studies (48 to 297 lines). The delayed plateau in $r_{MP}$ in Fig. 1 was then due to a combination of a larger $N_M$ and a larger $N$, as found by Muir (2007). The

second reason is that the current study focused on the GCA model whereas the Lorenzana and Bernardo (2009) and Combs and Bernardo (2013a) studies used the A/B model. As discussed in earlier, the lower initial $r^2$ in the training populations for the GCA model than for the A/B model allows a greater benefit of using more markers.

Further reduction in the cost of genotyping could occur if very few markers were assayed for the training and test populations. Prior to imputation, the marker subsets of 30 and 40 markers showed a significant decrease in R and $r_{MP}$ compared to the assayed marker densities (Table 12). For yield, the R and $r_{MP}$ for the subset of 30 markers imputed to 500 markers was not significantly lower than when imputation was based on the original $N_M$ of 49 to 100 SNP markers in the A/B crosses. For moisture, imputing from the original $N_M$ markers and imputing from the subset of 40 markers did not lead to significant differences in R and in $r_{MP}$. For test weight, imputing from the original $N_M$ markers and imputing from 50 markers did not lead to significant differences in R and in $r_{MP}$. These results indicate that genotyping at low marker coverage of about 50 markers and using marker imputation maintains the prediction accuracy in the $GCA_I$ model while saving costs.

On the other hand, we were unable to determine the current cost savings from genotyping 50 SNP markers instead of a few thousand SNP markers. A cost comparison of different SNP genotyping platforms has been published (Semagn et al., 2014), and general prices for SNP genotyping are available from different sources (e.g., UC Davis Genome Center, http://dnatech.genomecenter.ucdavis.edu/prices/; LGC, www.lgcgroup.com; Iowa State University Genomic Technologies Facility, http://www.plantgenomics.iastate.edu/fees.php). But the per-sample costs depend on the number of samples genotyped, and the number of samples would differ according to the

size of a breeding program. Nevertheless, we speculate that the costs would be lower if 384-SNP arrays are designed and used for each heterotic group or genetic background, than if each A/B cross is analyzed with 50 SNPs chosen for their polymorphism between parents A and B. In this scenario, all of the A/B populations within the same heterotic group would be assayed with the same 384-SNP array, with the expectation that at least 50 SNPs (out of the 384) will be found polymorphic in each A/B cross. Such an approach is likely to reduce the per-sample costs because the developmental costs are reduced and the cost savings are magnified when many individuals and populations are analyzed with the same SNP array.

*Recommendations*

In a previous study, we have strongly recommended the use of the GCA model because it allows genomewide selection in an A/B biparental population without having to phenotype any of the progeny in the A/B cross (Jacobson et al., 2014). In particular, the GCA model can be used to predict the testcross performance of $F_2$ plants for grain yield and other agronomic traits in maize. On the basis of the results of the current study, we further recommend that maize breeders (1) assay the inbred parents of the A/B, A/*, and */B populations with about 3000 SNP markers, (2) assay the A/B, A/*, and */B populations with a subset of about 50 SNP markers, (3) increase marker coverage of the A/B, A/*, and */B populations to about 1000 markers by imputation, and (4) use the $GCA_I$ model (with imputed markers) for genomewide selection within a biparental cross. Screening the parental inbreds with more than 1000 SNP loci (i.e., 3000 markers) is needed because many of the SNP loci would be monomorphic in different A/B crosses.

Our recommendation of assaying each maize population with only around 50 SNP markers may seem surprising, particularly when more than 50,000 SNPs can be assayed through the Illumina MaizeSNP50 BeadChip (Illumina, San Diego, CA) or through genotyping-by-sequencing (Elshire et al., 2011). Assaying 50 SNP markers in maize leads to a low marker density of one marker per 37 cM. However, the linkage disequilibrium is expected to be inherently high among the lines developed from the cross between two parental inbreds (Dudley, 1993). Due to limited recombination, large segments of chromosomes or even entire chromosomes are passed intact from the inbred parents to recombinant inbreds or doubled haploids in maize crosses (Smith et al., 2008). In one biparental cross in maize, the mean number of crossover events per chromosome was 1.0 among doubled haploids and 1.5 among recombinant inbreds (Smith et al., 2008). In 16 doubled haploid maize populations, the mean number of crossovers per chromosome was 1.4 (A. Jacobson, unpublished data, 2012). The high linkage disequilibrium that results from such limited recombination makes the four-step process we describe in the previous paragraph effective for biparental populations.

Table 7: Test and training populations for the A/B model and general combining ability (GCA) model in maize, with and without markers imputation.

| | Test population | | | | | | | | | | | | Training populations in the GCA model | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | $N_M$[†] | | LD with marker subset[‡] | | | | | | | | | | |
| Group[§] | A/B population | Tester | $N$[¶] | Locations | A/B | GCA | Assayed markers | 250 | 500 | 1000 | 2000 | 2911 | A/* | */B | $N_x$[#] | $N_{GCA}$[††] | LD[‡‡] |
| 1 | P1/P2 | T1 | 152 | 7 | 79 | 79 | 0.62 | 0.80 | 0.85 | 0.88 | 0.93 | 0.93 | 16 | 9 | 25 | 4066 | 0.29 |
| 1 | P3/P4 | T1 | 164 | 8 | 58 | 47 | 0.43 | 0.79 | 0.85 | 0.90 | 0.93 | 0.93 | 6 | 11 | 17 | 2940 | 0.38 |
| 1 | P4/P5 | T1 | 177 | 6 | 82 | 78 | 0.49 | 0.79 | 0.85 | 0.90 | 0.91 | 0.93 | 12 | 5 | 17 | 3175 | 0.29 |
| 1 | P6/P7 | T1 | 183 | 12 | 67 | 66 | 0.44 | 0.81 | 0.86 | 0.91 | 0.95 | 0.95 | 11 | 3 | 14 | 2705 | 0.35 |
| 1 | P3/P8 | T1 | 181 | 7 | 69 | 62 | 0.51 | 0.80 | 0.86 | 0.90 | 0.93 | 0.94 | 5 | 4 | 9 | 1493 | 0.42 |
| 1 | P1/P9 | T2 | 174 | 5 | 74 | 68 | 0.63 | 0.82 | 0.85 | 0.89 | 0.92 | 0.93 | 7 | 4 | 11 | 1558 | 0.49 |
| 1 | P5/P8 | T1 | 148 | 6 | 74 | 64 | 0.36 | 0.80 | 0.86 | 0.90 | 0.93 | 0.94 | 8 | 4 | 12 | 1623 | 0.44 |
| 1 | P9/P10 | T2 | 152 | 8 | 68 | 63 | 0.58 | 0.76 | 0.82 | 0.86 | 0.91 | 0.91 | 5 | 5 | 10 | 1794 | 0.35 |
| 1 | P11/P12 | T1 | 182 | 8 | 91 | 53 | 0.45 | 0.74 | 0.83 | 0.90 | 0.94 | 0.94 | 2 | 5 | 7 | 935 | 0.39 |
| 1 | P13/P14 | T3 | 178 | 8 | 86 | 82 | 0.64 | 0.82 | 0.87 | 0.89 | 0.91 | 0.91 | 4 | 3 | 7 | 1256 | 0.56 |
| 1 | P2/P15 | T3 | 160 | 5 | 89 | 68 | 0.57 | 0.68 | 0.83 | 0.89 | 0.92 | 0.94 | 5 | 3 | 8 | 982 | 0.53 |
| 1 | P16/P13 | T3 | 178 | 7 | 53 | 47 | 0.59 | 0.81 | 0.86 | 0.90 | 0.93 | 0.93 | 4 | 2 | 6 | 1058 | 0.52 |
| 1 | P17/P18 | T1 | 185 | 7 | 87 | 54 | 0.50 | 0.77 | 0.83 | 0.88 | 0.92 | 0.92 | 1 | 3 | 4 | 524 | 0.52 |
| 1 | P19/P20 | T4 | 186 | 5 | 100 | 67 | 0.52 | 0.78 | 0.84 | 0.89 | 0.92 | 0.93 | 2 | 2 | 4 | 676 | 0.51 |
| 2 | P21/P22 | T5 | 173 | 8 | 69 | 69 | 0.51 | 0.79 | 0.84 | 0.88 | 0.90 | 0.93 | 14 | 12 | 26 | 4357 | 0.43 |
| 2 | P23/P24 | T6 | 174 | 7 | 49 | 44 | 0.56 | 0.81 | 0.87 | 0.90 | 0.92 | 0.94 | 9 | 7 | 16 | 2860 | 0.55 |
| 2 | P25/P22 | T5 | 169 | 8 | 72 | 69 | 0.44 | 0.75 | 0.83 | 0.88 | 0.91 | 0.94 | 13 | 4 | 17 | 2912 | 0.51 |
| 2 | P26/P27 | T6 | 184 | 6 | 66 | 60 | 0.60 | 0.79 | 0.85 | 0.90 | 0.93 | 0.94 | 10 | 6 | 16 | 2587 | 0.53 |
| 2 | P23/P25 | T5 | 168 | 7 | 68 | 65 | 0.40 | 0.80 | 0.87 | 0.90 | 0.93 | 0.94 | 4 | 12 | 16 | 2558 | 0.49 |
| 2 | P24/P26 | T6 | 183 | 6 | 66 | 66 | 0.47 | 0.77 | 0.84 | 0.89 | 0.92 | 0.94 | 7 | 10 | 17 | 2863 | 0.5 |

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2 | P28/P27 | T6 | 180 | 8 | 49 | 48 | 0.43 | 0.80 | 0.87 | 0.91 | 0.94 | 0.95 | 6 | 3 | 9 | 1510 | 0.57 |
| 2 | P29/P27 | T6 | 175 | 7 | 69 | 61 | 0.56 | 0.81 | 0.88 | 0.91 | 0.93 | 0.95 | 4 | 6 | 10 | 1698 | 0.57 |
| 2 | P29/P30 | T6 | 183 | 5 | 98 | 77 | 0.53 | 0.78 | 0.85 | 0.90 | 0.91 | 0.94 | 4 | 6 | 10 | 1801 | 0.59 |
| 2 | P31/P32 | T7 | 170 | 8 | 63 | 57 | 0.39 | 0.76 | 0.83 | 0.88 | 0.90 | 0.93 | 2 | 5 | 7 | 1251 | 0.52 |
| 2 | P33/P34 | T8 | 181 | 7 | 85 | 54 | 0.60 | 0.83 | 0.92 | 0.92 | 0.93 | 0.95 | 2 | 2 | 4 | 715 | 0.6 |
| 2 | P35/P36 | T9 | 139 | 4 | 62 | 48 | 0.37 | 0.58 | 0.65 | 0.88 | 0.90 | 0.92 | 3 | 2 | 5 | 619 | 0.61 |
| 2 | P37/P38 | T10 | 183 | 5 | 74 | 58 | 0.50 | 0.81 | 0.86 | 0.90 | 0.92 | 0.93 | 2 | 2 | 4 | 532 | 0.59 |

†$N_{M,}$ number of markers in the A/B test population. Markers for the GCA model were removed if the marker was not present in at least two A/* and */B populations. Mean $r^2$ of adjacent SNP markers is listed in parentheses for the A/B population.

‡LD, mean $r^2$ of adjacent SNP markers for each marker subset within each population.

§Heterotic group.

¶$N$, number of $F_3$ lines in the A/B test population.

#$N_X$, number of biparental crosses in the training population for the GCA model.

††$N_{GCA}$, number of $F_3$ lines in the training population for the GCA model.

‡‡LD, mean $r^2$ of adjacent SNP markers for each marker subset within each pooled training population for the GCA model.

Table 8: Mean and range (in parentheses) of response to selection (R) and prediction accuracy ($r_{MP}$) across 27 test populations in maize.

| | Grain yield ($h^2$=0.40)† | | Moisture ($h^2$=0.67) | | Test weight ($h^2$=0.55) | |
|---|---|---|---|---|---|---|
| Method‡ | R (Mg ha$^{-1}$) | $r_{MP}$ | R (g kg$^{-1}$) | $r_{MP}$ | R (kg hL$^{-1}$) | $r_{MP}$ |
| Phenotypic selection | 0.25$^{a}$§ (0.03,0.48) | 0.26$^{a}$ (0.13,0.53) | -8$^{a}$ (-17,-2) | 0.54$^{a}$ (0.32.0.74) | 0.58$^{a}$ (0.16,1.09) | 0.39$^{a}$ (0.17,0.72) |
| A/B | 0.17$^{b}$ (-0.15,0.48) | 0.17$^{b}$ (-0.06,0.39) | -6$^{ab}$ (-16,1) | 0.39$^{bc}$ (0.05,0.67) | 0.43$^{bc}$ (0.06,0.85) | 0.30$^{bc}$ (0.06,0.60) |
| A/B$_I$ | 0.19$^{ab}$ (-0.12,0.46) | 0.17$^{b}$ (-0.11,0.40) | -6$^{ab}$ (-17,2) | 0.44$^{b}$ (-0.13,0.69) | 0.41$^{bc}$ (-0.01,0.79) | 0.33$^{abc}$ (0.05,0.59) |
| GCA | 0.16$^{b}$ (-0.14,0.42) | 0.15$^{b}$ (-0.04,0.40) | -5$^{b}$ (-12,0) | 0.33$^{c}$ (-0.08,0.54) | 0.34$^{c}$ (-0.09,0.78) | 0.26$^{c}$ (-0.03,0.50) |
| GCA$_I$ | 0.22$^{ab}$ (0.02,0.51) | 0.21$^{a}$ (-0.04,0.39) | -6$^{ab}$ (-13,0) | 0.44$^{b}$ (0.08,0.63) | 0.49$^{ab}$ (-0.03,0.84) | 0.34$^{ab}$ (-0.10,0.52) |
| GCA$_P$ | 0.18$^{ab}$ (-0.07,0.40) | 0.21$^{a}$ (-0.04,0.38) | -6$^{ab}$ (-10,1) | 0.44$^{b}$ (-0.07,0.64) | 0.49$^{ab}$ (-0.04,0.94) | 0.36$^{ab}$ (-0.05,0.60) |
| LSD | 0.078 | 0.059 | 1.97 | 0.077 | 0.13 | 0.073 |

†Heritability ($h^2$) on an entry-mean basis.

‡The R and $r_{MP}$ values were for phenotypic selection, A/B model, A/B model with imputed markers (A/B$_I$), general combining ability (GCA) model, GCA model with imputed markers (GCA$_I$), and GCA model with pooled $F_3$ lines (GCA$_P$).

§Within a column, estimates with a common letter were not significantly different (P=0.05).

Table 9: Response to selection (R) and prediction accuracy ($r_{MP}$) for grain yield with phenotypic selection (PS), A/B model, A/B model with imputed markers ($A/B_I$), general combining ability (GCA) model, GCA model with imputed markers ($GCA_I$), and GCA model with pooled $F_3$ lines ($GCA_P$) for genomewide selection in maize.

| Test population | $h^{2\dagger}$ | R (Mg ha$^{-1}$) | | | | | | $r_{MP}$ | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | PS | A/B | $A/B_I$ | GCA | $GCA_I$ | $GCA_P$ | PS | A/B | $A/B_I$ | GCA | $GCA_I$ | $GCA_P$ |
| P1/P2 | 0.61 | 0.45 | 0.48 | 0.41 | 0.42 | 0.31 | 0.35 | 0.45 | 0.27 | 0.21 | 0.31 | 0.31 | 0.36 |
| P3/P4 | 0.31 | 0.25 | 0.10 | 0.15 | 0.05 | 0.14 | 0.15 | 0.19 | 0.05 | 0.14 | 0.10 | 0.23 | 0.25 |
| P4/P5 | 0.46 | 0.37 | 0.18 | 0.19 | 0.34 | 0.30 | 0.20 | 0.31 | 0.22 | 0.19 | 0.23 | 0.27 | 0.25 |
| P6/P7 | 0.49 | 0.33 | 0.30 | 0.34 | 0.21 | 0.23 | 0.19 | 0.34 | 0.26 | 0.37 | 0.15 | 0.26 | 0.20 |
| P3/P8 | 0.42 | 0.17 | 0.11 | 0.15 | 0.12 | 0.16 | 0.20 | 0.27 | 0.09 | 0.13 | 0.16 | 0.14 | 0.21 |
| P1/ P9 | 0.39 | 0.07 | 0.28 | 0.29 | 0.33 | 0.36 | 0.28 | 0.25 | 0.34 | 0.35 | 0.40 | 0.39 | 0.36 |
| P5/P8 | 0.42 | 0.40 | 0.45 | 0.45 | 0.35 | 0.51 | 0.40 | 0.27 | 0.30 | 0.33 | 0.17 | 0.32 | 0.31 |
| P9/P10 | 0.36 | 0.22 | 0.08 | 0.08 | -0.01$^{NS\ddagger}$ | 0.03 | -0.07 | 0.22 | 0.23 | 0.05 | 0.05 | -0.04 | -0.04 |
| P11/P12 | 0.39 | 0.18 | 0.17 | 0.24 | -0.09 | 0.39 | 0.31 | 0.25 | 0.15 | 0.19 | 0.03 | 0.26 | 0.28 |
| P13/P14 | 0.52 | 0.35 | 0.39 | 0.39 | 0.11 | 0.04 | -0.01$^{NS}$ | 0.35 | 0.39 | 0.40 | 0.08 | 0.18 | 0.14 |
| P2/P15 | 0.30 | 0.26 | 0.24 | 0.34 | 0.14 | 0.20 | 0.13 | 0.18 | 0.23 | 0.33 | 0.12 | 0.26 | 0.20 |
| P16/P13 | 0.41 | 0.36 | 0.25 | 0.21 | 0.17 | 0.13 | 0.27 | 0.26 | 0.30 | 0.27 | 0.25 | 0.29 | 0.29 |
| P17/P18 | 0.43 | 0.39 | 0.26 | 0.35 | -0.04 | 0.42 | 0.16 | 0.29 | 0.20 | 0.23 | 0.18 | 0.31 | 0.26 |
| P19/P20 | 0.22 | 0.05 | 0.24 | 0.25 | 0.31 | 0.16 | 0.11 | 0.13 | 0.15 | 0.24 | 0.19 | 0.22 | 0.15 |
| P21/P22 | 0.50 | 0.35 | 0.28 | 0.31 | 0.30 | 0.27 | 0.38 | 0.34 | 0.16 | 0.21 | 0.15 | 0.24 | 0.23 |
| P23/P24 | 0.24 | 0.15 | 0.04 | -0.02 | 0.19 | 0.04 | -0.05 | 0.15 | 0.02 | -0.05 | -0.04 | -0.01$^{NS}$ | -0.02 |
| P25/P22 | 0.47 | 0.29 | 0.16 | 0.24 | 0.24 | 0.42 | 0.31 | 0.32 | 0.16 | 0.24 | 0.21 | 0.29 | 0.31 |
| P26/P27 | 0.24 | 0.15 | 0.17 | 0.18 | 0.12 | 0.14 | 0.14 | 0.14 | 0.15 | 0.11 | 0.22 | 0.23 | 0.25 |
| P23/P25 | 0.70 | 0.48 | 0.16 | 0.20 | 0.38 | 0.33 | 0.28 | 0.53 | 0.22 | 0.22 | 0.35 | 0.37 | 0.38 |
| P24/P26 | 0.47 | 0.34 | 0.06 | 0.07 | 0.08 | 0.18 | 0.21 | 0.31 | 0.05 | 0.12 | 0.05 | 0.18 | 0.15 |
| P28/P27 | 0.40 | 0.18 | -0.05 | 0.08 | 0.29 | 0.14 | 0.10 | 0.25 | 0.12 | 0.10 | 0.19 | 0.19 | 0.15 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P29/P27 | 0.25 | 0.19 | 0.02 | -0.01$^{NS}$ | 0.00$^{NS}$ | 0.30 | 0.18 | 0.15 | 0.03 | -0.01$^{NS}$ | 0.09 | 0.18 | 0.19 |
| P29/P30 | 0.25 | 0.18 | 0.05 | 0.04 | 0.14 | 0.30 | 0.11 | 0.13 | 0.07 | 0.05 | 0.14 | 0.22 | 0.22 |
| P33/P34 | 0.53 | 0.42 | -0.11 | -0.06 | -0.14 | 0.15 | 0.18 | 0.37 | 0.09 | -0.01$^{NS}$ | 0.06 | 0.17 | 0.19 |
| P35/P36 | 0.27 | 0.15 | -0.15 | -0.12 | 0.09 | 0.02 | -0.04 | 0.16 | -0.06 | -0.11 | 0.03 | 0.07 | 0.00$^{NS}$ |
| P37/P38 | 0.44 | 0.12 | 0.43 | 0.46 | 0.08 | 0.03 | 0.12 | 0.29 | 0.24 | 0.25 | 0.09 | 0.01$^{NS}$ | 0.13 |
| P41/P42 | 0.24 | 0.03 | 0.04 | 0.02 | 0.23 | 0.24 | 0.21 | 0.13 | 0.12 | 0.03 | 0.21 | 0.23 | 0.18 |

†Heritability ($h^2$) on an entry-mean basis.

‡NS, not significantly different from zero (P=0.05). All other estimates of R and $r_{MP}$ were significant.

Table 10: Response to selection (R) and prediction accuracy ($r_{MP}$) for moisture with phenotypic selection (PS), A/B model, A/B model with imputed markers ($A/B_I$), general combining ability (GCA) model, GCA model with imputed markers ($GCA_I$), and GCA model with pooled $F_3$ lines ($GCA_P$) for genomewide selection in maize.

| Test population | $h^{2\dagger}$ | R (g kg$^{-1}$) | | | | | | $r_{MP}$ | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | PS | A/B | $A/B_I$ | GCA | $GCA_I$ | $GCA_P$ | PS | A/B | $A/B_I$ | GCA | $GCA_I$ | $GCA_P$ |
| P1/P2 | 0.58 | -5 | -5 | -3 | -4 | -4 | -4 | 0.42 | 0.37 | 0.35 | 0.48 | 0.48 | 0.53 |
| P3/P4 | 0.74 | -11 | -8 | -7 | -8 | -10 | -9 | 0.59 | 0.46 | 0.46 | 0.44 | 0.49 | 0.49 |
| P4/P5 | 0.76 | -7 | -5 | -5 | -2 | -5 | -5 | 0.65 | 0.48 | 0.56 | 0.22 | 0.56 | 0.54 |
| P6/P7 | 0.83 | -11 | -12 | -10 | -8 | -7 | -10 | 0.72 | 0.37 | 0.67 | 0.46 | 0.51 | 0.64 |
| P3/P8 | 0.72 | -7 | -6 | -5 | -6 | -6 | -5 | 0.57 | 0.41 | 0.43 | 0.39 | 0.50 | 0.46 |
| P1/ P9 | 0.55 | -3 | -3 | -3 | -4 | -4 | -4 | 0.40 | 0.26 | 0.38 | 0.39 | 0.46 | 0.43 |
| P5/P8 | 0.56 | -2 | -3 | -2 | -2 | -2 | -2 | 0.42 | 0.36 | 0.36 | 0.22 | 0.32 | 0.29 |
| P9/P10 | 0.79 | -14 | -11 | -11 | -6 | -6 | -10 | 0.66 | 0.47 | 0.53 | 0.26 | 0.38 | 0.44 |
| P11/P12 | 0.84 | -10 | -9 | -9 | -5 | -8 | -7 | 0.74 | 0.57 | 0.66 | 0.34 | 0.63 | 0.56 |
| P13/P14 | 0.68 | -4 | -2 | -3 | -2 | -3 | -3 | 0.54 | 0.36 | 0.52 | 0.26 | 0.38 | 0.38 |
| P2/P15 | 0.56 | -2 | -4 | -3 | -3 | -4 | -3 | 0.40 | 0.31 | 0.42 | 0.37 | 0.49 | 0.49 |
| P16/P13 | 0.76 | -9 | -10 | -9 | -8 | -8 | -9 | 0.62 | 0.58 | 0.61 | 0.54 | 0.60 | 0.62 |
| P17/P18 | 0.51 | -17 | -16 | -17 | -5 | -13 | -9 | 0.62 | 0.67 | 0.69 | 0.25 | 0.62 | 0.54 |
| P19/P20 | 0.55 | -6 | -3 | -3 | -2 | -4 | -5 | 0.40 | 0.22 | 0.27 | 0.17 | 0.32 | 0.36 |
| P21/P22 | 0.46 | -5 | -7 | -5 | -6 | -6 | -5 | 0.32 | 0.38 | 0.38 | 0.38 | 0.37 | 0.37 |
| P23/P24 | 0.63 | -7 | -5 | -4 | -4 | -4 | -4 | 0.47 | 0.34 | 0.35 | 0.28 | 0.29 | 0.30 |
| P25/P22 | 0.66 | -9 | -6 | -7 | -4 | -7 | -9 | 0.51 | 0.36 | 0.36 | 0.23 | 0.39 | 0.43 |
| P26/P27 | 0.73 | -9 | -6 | -6 | -7 | -7 | -7 | 0.58 | 0.48 | 0.54 | 0.30 | 0.46 | 0.60 |
| P23/P25 | 0.72 | -7 | -5 | -6 | -7 | -7 | -7 | 0.60 | 0.35 | 0.40 | 0.50 | 0.52 | 0.52 |
| P24/P26 | 0.71 | -7 | -6 | -6 | -7 | -6 | -5 | 0.56 | 0.38 | 0.44 | 0.45 | 0.41 | 0.41 |
| P28/P27 | 0.81 | -14 | -11 | -13 | -4 | -12 | -10 | 0.70 | 0.56 | 0.62 | 0.31 | 0.52 | 0.53 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P29/P27 | 0.74 | -6 | -5 | -5 | -4 | -4 | -6 | 0.62 | 0.49 | 0.55 | 0.51 | 0.57 | 0.58 |
| P29/P30 | 0.74 | -5 | -4 | -4 | -4 | -6 | -6 | 0.47 | 0.44 | 0.46 | 0.35 | 0.53 | 0.53 |
| P33/P34 | 0.53 | -10 | -4 | -4 | -6 | -4 | -6 | 0.40 | 0.12 | 0.16 | 0.15 | 0.12 | 0.14 |
| P35/P36 | 0.59 | -4 | 1 | 2 | 0 | 0 | 1 | 0.43 | 0.05 | -0.13 | -0.08 | 0.08 | -0.07 |
| P37/P38 | 0.58 | -9 | -6 | -6 | -5 | -8 | -6 | 0.49 | 0.24 | 0.28 | 0.29 | 0.33 | 0.37 |
| P41/P42 | 0.73 | -10 | -9 | -11 | -12 | -11 | -10 | 0.61 | 0.55 | 0.61 | 0.47 | 0.57 | 0.52 |

[†]Heritability ($h^2$) on an entry-mean basis.

Table 11: Response to selection (R) and prediction accuracy ($r_{MP}$) for test weight with phenotypic selection (PS), A/B model, A/B model with imputed markers ($A/B_I$), general combining ability (GCA) model, GCA model with imputed markers ($GCA_I$), and GCA model with pooled $F_3$ lines ($GCA_P$) for genomewide selection in maize.

| Test population | $h^{2\dagger}$ | R (kg hL$^{-1}$) | | | | | | $r_{MP}$ | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | PS | A/B | $A/B_I$ | GCA | $GCA_I$ | $GCA_P$ | PS | A/B | $A/B_I$ | GCA | $GCA_I$ | $GCA_P$ |
| P1/P2 | 0.32 | 0.21 | 0.25 | 0.35 | 0.32 | 0.13 | 0.32 | 0.21 | 0.22 | 0.25 | 0.32 | 0.21 | 0.39 |
| P3/P4 | 0.52 | 0.61 | 0.34 | 0.44 | 0.16 | 0.59 | 0.50 | 0.36 | 0.25 | 0.32 | 0.10 | 0.36 | 0.33 |
| P4/P5 | 0.34 | 0.46 | 0.14 | 0.26 | 0.52 | 0.48 | 0.54 | 0.23 | 0.09 | 0.16 | 0.19 | 0.32 | 0.30 |
| P6/P7 | 0.82 | 1.09 | 0.75 | 0.40 | 0.45 | 0.68 | 0.48 | 0.72 | 0.11 | 0.50 | 0.40 | 0.47 | 0.46 |
| P3/P8 | 0.67 | 0.80 | 0.63 | 0.56 | 0.27 | 0.46 | 0.58 | 0.51 | 0.45 | 0.44 | 0.37 | 0.48 | 0.50 |
| P1/ P9 | 0.46 | 0.48 | 0.16 | 0.21 | 0.22 | 0.30 | 0.37 | 0.32 | 0.16 | 0.22 | 0.27 | 0.26 | 0.29 |
| P5/P8 | 0.50 | 0.50 | 0.37 | 0.17 | 0.62 | 0.49 | 0.39 | 0.34 | 0.28 | 0.20 | 0.28 | 0.29 | 0.28 |
| P9/P10 | 0.50 | 0.72 | 0.39 | 0.32 | 0.57 | 0.49 | 0.48 | 0.35 | 0.29 | 0.24 | 0.34 | 0.41 | 0.40 |
| P11/P12 | 0.51 | 0.45 | 0.29 | 0.32 | 0.11 | 0.44 | 0.45 | 0.35 | 0.26 | 0.33 | 0.14 | 0.33 | 0.43 |
| P13/P14 | 0.61 | 0.37 | 0.32 | 0.39 | 0.31 | 0.38 | 0.35 | 0.45 | 0.27 | 0.44 | 0.25 | 0.36 | 0.36 |
| P2/P15 | 0.34 | 0.24 | 0.09 | 0.07 | 0.24 | 0.49 | 0.34 | 0.20 | 0.06 | 0.09 | 0.20 | 0.31 | 0.28 |
| P16/P13 | 0.70 | 0.66 | 0.78 | 0.77 | 0.70 | 0.72 | 0.71 | 0.54 | 0.6 | 0.59 | 0.45 | 0.45 | 0.43 |
| P17/P18 | 0.27 | 0.27 | 0.83 | 0.70 | 0.05 | 0.38 | 0.41 | 0.22 | 0.51 | 0.49 | 0.03 | 0.18 | 0.30 |
| P19/P20 | 0.64 | 0.91 | 0.5 | 0.45 | 0.18 | 0.66 | 0.67 | 0.49 | 0.18 | 0.32 | 0.05 | 0.39 | 0.37 |
| P21/P22 | 0.56 | 0.68 | 0.46 | 0.43 | 0.63 | 0.32 | 0.63 | 0.40 | 0.33 | 0.39 | 0.38 | 0.33 | 0.36 |
| P23/P24 | 0.48 | 0.48 | 0.30 | 0.31 | 0.16 | 0.31 | 0.27 | 0.33 | 0.23 | 0.23 | 0.24 | 0.18 | 0.38 |
| P25/P22 | 0.63 | 0.57 | 0.31 | 0.36 | 0.32 | 0.61 | 0.49 | 0.46 | 0.25 | 0.31 | 0.14 | 0.37 | 0.36 |
| P26/P27 | 0.68 | 0.75 | 0.85 | 0.79 | 0.64 | 0.79 | 0.94 | 0.53 | 0.55 | 0.56 | 0.50 | 0.52 | 0.60 |
| P23/P25 | 0.65 | 0.96 | 0.68 | 0.72 | 0.78 | 0.78 | 0.77 | 0.47 | 0.36 | 0.41 | 0.35 | 0.36 | 0.39 |
| P24/P26 | 0.71 | 0.83 | 0.69 | 0.66 | 0.56 | 0.72 | 0.55 | 0.57 | 0.49 | 0.51 | 0.42 | 0.46 | 0.53 |
| P28/P27 | 0.48 | 0.47 | 0.17 | 0.29 | -0.01$^{NS\ddagger}$ | 0.55 | 0.35 | 0.34 | 0.18 | 0.29 | 0.18 | 0.32 | 0.29 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P29/P27 | 0.58 | 0.46 | 0.51 | 0.47 | 0.49 | 0.47 | 0.48 | 0.41 | 0.43 | 0.43 | 0.40 | 0.36 | 0.37 |
| P29/P30 | 0.58 | 0.16 | 0.06 | 0.12 | 0.03 | 0.30 | 0.32 | 0.17 | 0.14 | 0.19 | 0.31 | 0.44 | 0.44 |
| P33/P34 | 0.61 | 0.86 | 0.38 | 0.04 | 0.25 | 0.84 | 0.71 | 0.45 | 0.32 | 0.07 | 0.20 | 0.24 | 0.23 |
| P35/P36 | 0.27 | 0.30 | 0.10 | -0.01$^{NS}$ | -0.09 | -0.03 | -0.04 | 0.18 | 0.06 | 0.05 | 0.01$^{NS}$ | -0.10 | -0.05 |
| P37/P38 | 0.61 | 0.46 | 0.73 | 0.69 | 0.39 | 0.35 | 0.53 | 0.46 | 0.55 | 0.54 | 0.38 | 0.37 | 0.47 |
| P41/P42 | 0.71 | 0.86 | 0.65 | 0.75 | 0.40 | 0.56 | 0.61 | 0.55 | 0.37 | 0.50 | 0.25 | 0.32 | 0.34 |

† Heritability ($h^2$) on an entry-mean basis.

‡NS, not significantly different from zero ($P$ = 0.05). All other estimates of R and $r_{MP}$ were significant.

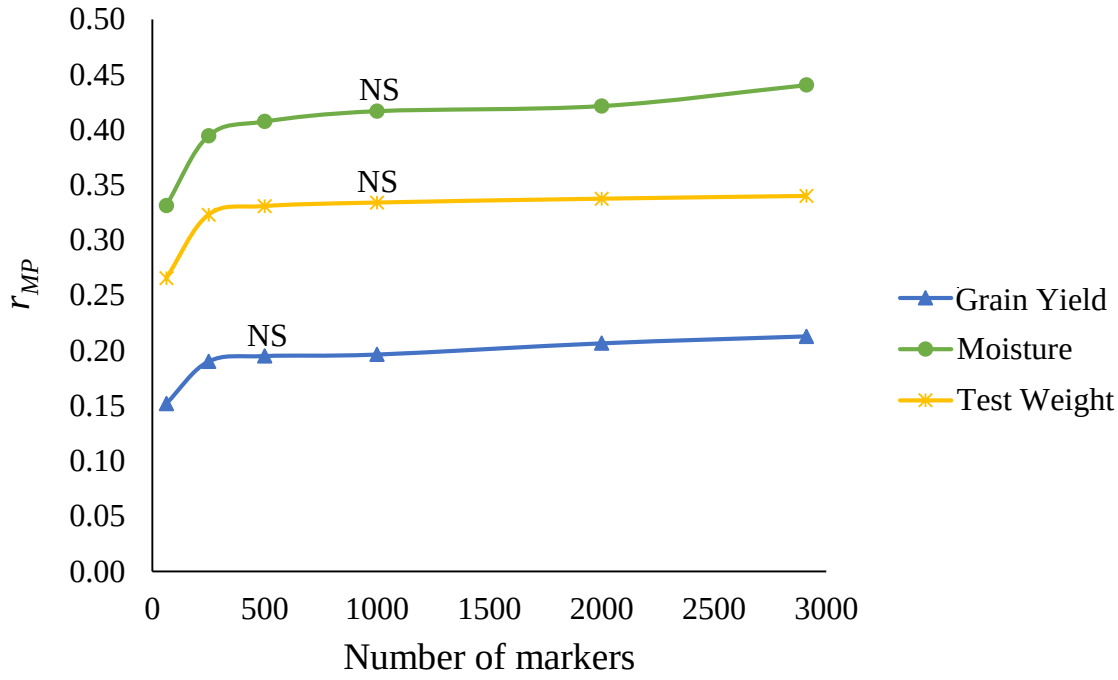
Table 12: Mean and range (in parentheses) of response to selection (R) and prediction accuracy ($r_{MP}$) across 27 test populations in maize for imputation of markers from 30, 40, 50 marker subsets.

| | | | Grain yield (Mg ha$^{-1}$) | | Moisture (g kg$^{-1}$) | | Test weight (kg hL$^{-1}$) | |
|---|---|---|---|---|---|---|---|---|
| Initial markers | Imputation | | R | $r_{MP}$ | R | $r_{MP}$ | R | $r_{MP}$ |
| 30 | None | | 0.08$^{b\dagger}$ (-0.62,0.31) | 0.08$^{b}$ (-0.12,0.27) | -3$^{b}$ (-10,0) | 0.21$^{c}$ (-0.08,0.47) | 0.11$^{c}$ (-0.36,0.50) | 0.13$^{b}$ (-0.08,0.44) |
| 40 | | | 0.08$^{b}$ (-0.12,0.32) | 0.09$^{b}$ (-0.10,0.29) | -3$^{b}$ (-9,0) | 0.26$^{bc}$ (0,0.51) | 0.18$^{bc}$ (-0.37,0.53) | 0.16$^{b}$ (-0.09,0.37) |
| 50 | | | 0.08$^{b}$ (-0.35,0.43) | 0.12$^{ab}$ (-0.08,0.33) | -4$^{ab}$ (-11,0) | 0.29$^{ab}$ (0,0.51) | 0.28$^{ab}$ (-0.20,0.75) | 0.20$^{ab}$ (0.02,0.42) |
| Number assayed | | | 0.16$^{a}$ (-0.14,0.42) | 0.15$^{a}$ (-0.04,0.40) | -5$^{a}$ (-12,0) | 0.33$^{a}$ (-0.08,0.54) | 0.34$^{a}$ (-0.09,0.78) | 0.26$^{a}$ (-0.03,0.50) |
| | | LSD | 0.087 | 0.056 | 1.33 | 0.067 | 0.12 | 0.066 |
| 30 | Conditional probability imputation$^{\ddagger}$ | | 0.19$^{a}$ (-0.27,0.40) | 0.15$^{a}$ (-0.06,0.32) | -5$^{b}$ (-12,0) | 0.34$^{b}$ (0.00,0.54) | 0.31$^{b}$ (-0.34,0.84) | 0.25$^{b}$ (-0.01,0.50) |
| 40 | | | 0.23$^{a}$ (-0.09,0.41) | 0.18$^{a}$ (-0.05,0.36) | -5$^{ab}$ (-11,2) | 0.37$^{ab}$ (0.00,0.58) | 0.32$^{b}$ (-0.46,0.66) | 0.26$^{b}$ (0.01,0.50) |
| 50 | | | 0.24$^{a}$ (-0.10,0.44) | 0.18$^{a}$ (-0.07,0.40) | -6$^{ab}$ (-13,1) | 0.39$^{ab}$ (-0.01,0.62) | 0.40$^{ab}$ (-0.11,0.87) | 0.30$^{ab}$ (-0.01,0.54) |
| Number assayed | | | 0.26$^{a}$ (-0.02,0.49) | 0.19$^{a}$ (-0.04,0.39) | -7$^{a}$ (-13,-1) | 0.42$^{a}$ (-0.10,0.62) | 0.49$^{a}$ (-0.33,0.77) | 0.33$^{a}$ (-0.01,0.54) |
| | | LSD | 0.074 | 0.056 | 1.76 | 0.076 | 0.14 | 0.063 |

$^{\dagger}$Within a column, estimates with a common letter were not significantly different (P=0.05).

$^{\ddagger}$Imputation to $N_{M(Sub)}$=500 markers for grain yield and $N_{M(Sub)}$=1000 markers for moisture.

Figure 1: Prediction accuracy ($r_{MP}$) of the general combining ability model with marker imputation ($GCA_I$) for subsets of $N_{M(Sub)}$=250, 500, 1000 and 2000 markers out of 2911 markers. NS signifies the marker coverage in which there were no further significant increase in $r_{MP}$.



## Chapter 3: Minimal loss of genetic diversity after genomewide selection within biparental maize populations

Concerns have been raised that genomewide selection may hasten the loss of genetic diversity in plant breeding programs. Our objective was to determine if genomewide selection and phenotypic selection lead to different levels of genetic similarity among the selected lines within a biparental population. The best 5, 10, 25 and 50% of $F_3$ lines within each of 27 maize (*Zea mays* L.) biparental populations were identified by phenotypic selection for testcross performance and by genomewide selection. Without any selection, the mean genetic similarity among lines within a population was 0.52 and the maximum similarity among lines was 0.71. Averaged across the 27 populations, phenotypic selection for grain yield, moisture, and an index of these two traits did not cause a significant increase in genetic similarity among the selected lines. Likewise, genomewide selection of the best 50% of the lines did not lead to a significant increase in genetic similarity. In contrast, genomewide selection of the best 5% of lines significantly increased the mean similarity from 0.52 to 0.57. For comparison, the mean similarity was 0.68 among the 5% most similar lines. The minimal increase in genetic similarity with genomewide selection was attributed to the absence of lines with the perfect or near-perfect marker profile in the biparental populations. The general level of genetic diversity within the training population had no effect on the genetic similarity among the selected lines. We conclude that genomewide selection causes only a minimal loss in genetic diversity within biparental populations.

## Introduction

Genetic diversity is needed to sustain long-term gains. Maize (*Zea mays* L.) germplasm has become less diverse over time because breeding programs have typically used only a few progenitor inbreds (Darrah and Zuber, 1986; Smith, 1988; Hallauer, 1990; Troyer, 1996). This narrowing of the current breeding germplasm has become a concern with regards to future increases in maize productivity and an increased genetic vulnerability to biotic and abiotic stresses (Smith, 1988; Troyer et al., 1988; Tanksley, 1997).

Selection within a maize biparental cross has been traditionally based on phenotypic information (Hallauer, 1990). Genomewide selection allows for selection based on marker-predicted genotypic values (Meuwissen et al., 2001) and takes advantage of the lower costs of genotyping than of phenotyping in maize (Bernardo and Yu, 2007; Heffner et al., 2010). Studies in maize have shown that genomewide selection is sufficiently accurate (Lorenzana and Bernardo, 2009; Heffner et al., 2010; Heslot et al., 2012; Windhausen et al., 2012; Combs and Bernardo, 2013a, 2013b; Riedelsheimer et al., 2013; Lian et al., 2014). At the University of Minnesota, we found substantial observed responses to genomewide recurrent selection in two maize populations (Massman et al., 2012; Combs and Bernardo, 2013a), and to genomewide selection of the best lines in 30 maize populations (Jacobson et al., 2014, 2015).

Whereas the above empirical studies have shown that genomewide selection is effective in changing the mean of a population, little empirical research has been done to determine the effect of genomewide selection on genetic diversity. Concerns have been raised within the maize seed industry (R. Bernardo, pers. comm., 2011) that because

genomewide selection exerts selection pressure directly at the marker level, it may erode genetic diversity more quickly compared with phenotypic selection. In other words, selection of individuals that carry the best combination of marker alleles (according to a specific prediction model) may lead to individuals that are highly similar to the desired marker profile and, consequently, to each other. Such a loss in genetic diversity is compounded when (1) a low cost of genotyping leads to a higher selection intensity, due to more individuals evaluated in genomewide selection than in phenotypic selection (Lorenz, 2013), and (2) multiple cycles of genomewide selection can be conducted per year in year-round nurseries or greenhouses (Bernardo and Yu, 2007; Heffner et al., 2010; Massman et al., 2012). A simulation study found that genomewide selection can indeed decrease genetic diversity across populations over multiple cycles of selection (Jannink, 2010).

To our knowledge, empirical studies have not been reported on the effect of genomewide selection on the genetic diversity within breeding populations in plants. Our objective in this study was to determine if genomewide selection and phenotypic selection lead to different levels of genetic similarity among the selected lines within a biparental population.

## Materials and Methods

### *Phenotypic and Marker Data*

Phenotypic and marker data for 969 biparental testcross populations were provided to us by Monsanto. The populations analyzed in this study and the criteria for choosing them were the same as those used by Jacobson et al. (2014, 2015). The $F_3$ lines in each population were evaluated for their testcross performance for grain yield (Mg $ha^{-1}$) and

moisture (g $kg^{-1}$) at 4 to 12 environments across the U.S. from 2001 to 2008. To determine if selection for multiple traits instead of a single trait affects genetic diversity, we combined information on grain yield and moisture into a retrospective selection index of I = (grain yield in Mg $ha^{-1}$) – 0.028 (grain moisture in g $kg^{-1}$), where I was the index value and –0.028 was the retrospective index weight previously used for grain moisture (with a weight of 1.0 for grain yield in Mg $ha^{-1}$) in a commercial maize breeding program (Bernardo, 1991).

The parents of the biparental populations were genotyped with 2911 single nucleotide polymorphism (SNP) markers, whereas the progeny within each population were genotyped with 49–100 SNP markers polymorphic between the two parents. On the basis of the conditional probability of marker genotypes given their flanking markers, marker imputation was conducted to obtain marker data for all 2911 SNP markers among all of the progeny in each cross (Jacobson et al., 2015). A SNP locus was excluded within each population if the locus was monomorphic between the two parental inbreds or if the minor allele frequency was less than 0.10. The imputed marker datasets were used for determining the prediction accuracy and gain from selection for the genomewide selection models. Only the original, non-imputed SNP markers were used to calculate genetic similarity.

*Selection Methods*

Within each of the 27 biparental crosses, we identified the best 5, 10, 25, and 50% of the lines through genomewide selection via two models [A/B model and general combining ability (GCA) model] and through phenotypic selection. The best lines were identified separately for grain yield, moisture, and the retrospective index.

In genomewide selection with the A/B model, the training population consisted of the population itself. The cross-validation procedures and calculation of prediction accuracy and selection response were described in detail by Jacobson et al. (2014, 2015). The prediction accuracy, which was the correlation between marker-predicted genotypic values and phenotypic values ($r_{MP}$) was calculated with a delete-one procedure along with cross-validation across environments as described by Jacobson et al. (2014). Marker effects were estimated by ridge regression-best linear unbiased prediction (RR-BLUP) using the package rrBLUP version 4.0 in R statistical software (Piepho, 2009; Endelman, 2011; R Development Core Team, 2012). In the delete-one method, the performance of each of the $N$ $F_3$ lines was predicted from RR-BLUP analysis of the remaining $N - 1$ lines. The cross-validation across environments was conducted to eliminate a bias present in the A/B model due to the test and training populations being evaluated in the same environments.

Selection was for high grain yield, low moisture, and high retrospective index value. The selection response (R) was calculated from the mean of the top 10% of $F_3$ lines with the best predicted performance for each trait. The mean performance of the best $F_3$ lines in the other half of the environments was denoted $y_{0.10}$. The R values were obtained as $y_{0.10} - \mu$, where $\mu$ was the population mean in the other half of the environments (Jacobson et al., 2014).

In genomewide selection with the GCA model, all available A/* and */B populations were used as a training population, with * indicating any inbred in the same heterotic group as A or B (Jacobson et al., 2014). For each of the 27 test populations, the A/B, A/*, and */B populations were all crossed to the same tester. Marker imputation was used in the GCA model (Jacobson et al, 2015), and imputed datasets of 2911 SNP markers

were used in the RR-BLUP analysis. Marker effects were estimated separately within each A/* and */B population and were averaged across the A/* and */B training populations. Cross-validation across environments was done for the A/B test population according to the same procedure for splitting environments used in the A/B model.

In phenotypic selection within an A/B population, the mean performance of the $N$ $F_3$ lines in half of the environments was considered the predictor of the performance of the same lines in the remaining half of the environments (Jacobson et al., 2014). The R and $r_{MP}$ were calculated the same as in the A/B model. For convenience, the prediction accuracy of phenotypic selection was also denoted by $r_{MP}$ even though the prediction of the performance did not involve marker effects.

*Genetic Similarity*

We studied how genetic similarity was affected by genomewide selection and phenotypic selection of the best 5, 10, 25, and 50% of the lines. For each of the three selection methods and three traits, we calculated the genetic similarity between each pair of lines within the selected subset of lines. We then calculated the mean similarity across all pairs within each selected subset, and the mean similarity was denoted by $S_{0.05}$, $S_{0.10}$, $S_{0.25}$, and $S_{0.5}$, where the subscripts indicated the proportion of lines selected. The mean genetic similarity without selection (denoted by $S_{1.0}$) was calculated as the mean similarity among all $N(N-1)/2$ pairs of lines within an A/B cross.

Genetic similarity between two lines was calculated as the simple matching coefficient (Sokal and Michener, 1958) among the four possible combinations of alleles carried by two $F_3$ lines at a SNP locus. Suppose the two alleles at a SNP locus are denoted by $x_1x_2$ in line X, and by $y_1y_2$ in line Y. The genetic similarity at the locus was the mean

simple matching coefficient between $x_1$ and $y_1$, $x_1$ and $y_2$, $x_2$ and $y_1$, and $x_2$ and $y_2$. Further suppose that the marker genotypes at a SNP locus are *MM*, *Mm*, and *mm*. At a single locus, the simple matching coefficient between lines was then as follows: (1) 1 between *MM* and *MM*; (2) 1 between *mm* and *mm*; (3) 0 between *MM* and *mm*; and (4) 0.50 between *Mm* and any other genotype (*MM*, *Mm*, or *mm*).

To have a benchmark for interpreting the $S_{0.05}$, $S_{0.10}$, $S_{0.25}$, $S_{0.50}$ values, we calculated the similarity when the lines were selected on the basis of marker similarity itself. First, we calculated the maximum genetic similarity between a pair of lines within the same A/B population. Second, we calculated the mean genetic similarity among the 5% of lines that were most similar to each other. Cluster analysis (Unweighted Pair Group Method with Arithmetic Mean method, implemented in R statistical software) of the $F_3$ lines within each A/B population was conducted on the basis of their genetic similarity (Sneath and Sokal, 1973). The first cluster that represented 5% of lines was identified from the dendrogram, and the mean similarity was calculated among these lines.

We conducted z-tests to determine if $S_{1.0}$ within each A/B population was significantly different (P = 0.50) from the expected similarity of 0.50. Least significant differences (LSD) (P = 0.05) for genetic similarity were calculated on the basis of the variance of the mean similarity across the 27 A/B crosses. The variances of R and $r_{MP}$ were obtained across the cross-validation repeats. These variances were used to calculate LSDs (P = 0.05) for the mean $r_{MP}$ and mean R. The proportion of lines selected was the same among the all 27 A/B crosses, but the number of lines in each population ranged from $N$ = 139 to 186 (Table 13). For a given proportion selected, the number of lines selected within each population therefore varied slightly among the 27 A/B populations. Selection of the

best 5% led to selection of 7 to 10 lines, whereas selection of the best 50% led to selection of the best 70 to 93 lines.

The correlation between $r_{MP}$ and the $S_{0.05}$, $S_{0\ .10}$, $S_{0.25}$, and $S_{0.50}$ values were calculated. The correlation between R and genetic similarity was also calculated. The R values were standardized by dividing it by the square root of the estimated testcross genetic variance ($V_G$) reported by Jacobson et al. (2014) for each population.

**Results and Discussion**

*Genetic Similarity after Phenotypic Selection and Genomewide Selection*

In theory, the expected genetic similarity among the segregating progeny in a biparental cross is 0.50 when all of the markers are polymorphic between the two inbred parents (A and B). The mean genetic similarity for the entire population (without selection) ranged from $S_{1.0}$ = 0.50 to 0.58, and had a mean of 0.52 across the 27 A/B test populations (Table 14). The $S_{1.0}$ values were significantly different from 0.50 for all of the test populations, except P1/P2, P6/P7, P2/P15, and P23/P25. The values for the observed and expected genetic similarity may have differed due to segregation distortion (Lu et al., 2002), genetic drift, or natural or artificial selection. Regardless of the underlying reasons, we considered the 0.02 mean deviation to be minor.

On average, phenotypic selection did not lead to a loss in genetic diversity within a biparental cross. Whereas the mean similarity across the 27 test populations was $S_{1.0}$ = 0.52 without selection, the mean genetic similarity among the best 5% of lines with phenotypic selection was $S_{0.05}$ = 0.53 (Table 14). None of the differences was statistically significant (P = 0.05) between the mean $S_{1.0}$ across the 27 A/B populations and the mean $S_{0.50}$ (best 50% selected), $S_{0.25}$ (best 25% selected), $S_{0.10}$ (best 10% selected), and $S_{0.05}$ (best 5%

selected) (Table 14). However, these results did not hold true for all 27 test populations: $S_{0.05}$ with phenotypic selection was significantly greater than $S_{1.0}$ in 6 populations for grain yield, 10 populations for moisture, and 11 populations for the retrospective index (Tables 15, 16 and 17).

In contrast to phenotypic selection, the two genomewide selection models (A/B model and GCA model) led to a loss in the genetic diversity among the selected lines, particularly when selection was stringent. When the best 5, 10%, or 25% of the lines were selected, the resulting $S_{0.05}$, $S_{0.10}$, and $S_{0.25}$ values averaged across the 27 A/B populations were significantly greater ($P = 0.05$) than $S_{1.0}$ (Table 14). In addition, the $S_{0.05}$, $S_{0.10}$, and $S_{0.25}$ values for the A/B and GCA models were significantly greater than the corresponding values for phenotypic selection. These results were consistent for grain yield, moisture, and the retrospective index. For grain yield, the mean $S_{0.05}$ was 0.53 with phenotypic selection and 0.57 with both the GCA model and A/B model (Table 14). The significant increases in $S_{0.05}$, $S_{0.10}$, and $S_{0.25}$ indicated that genomewide selection may retain less genetic diversity compared with phenotypic selection. But when the top 50% of the lines in the population were selected via genomewide selection, the mean $S_{0.50}$ values with selection for any of the traits were not significantly different from $S_{1.0}$ (Table 14).

Whereas stringent genomewide selection led to a statistically significant loss in genetic diversity, the loss was relatively small when compared with the range in the genetic similarity among all of the lines within an A/B population. Averaged across the 27 A/B test populations, the minimum genetic similarity among two random lines was 0.33 whereas the maximum genetic similarity among two random lines was 0.71. The mean similarity among the 5% of lines that were most similar to each other was 0.68. The mean

$S_{0.05}$ of 0.57 for the GCA model was therefore much lower than what would have been reached (0.68) if selection of the top 5% of lines was based on genetic similarity itself. This result indicated that although the loss of genetic diversity due to the GCA model was statistically significant, the amount of loss was minimal.

We attributed this minimal increase in genetic similarity with genomewide selection to the absence of lines that had the perfect or near-perfect marker profile in the biparental populations. If selection is highly effective in identifying the best candidates in a population, a loss in genetic diversity would naturally result from the retention of only those lines that have a high frequency of favorable alleles across all loci associated with a trait. Suppose that at the *i*th SNP locus, the marker allele from parent A is denoted by $M_i$ and the marker allele from parent B is denoted by $m_i$. Further suppose that the RR-BLUP analysis indicated that the most desirable marker profile, which represents a line that has all of the favorable marker alleles in the A/B cross, is $M_1M_1m_2m_2M_3M_3M_4M_4\ldots m_{2911}m_{2911}$. Genomewide selection would lead to a high similarity among the selected lines if there are lines in the A/B population that are either $M_1M_1m_2m_2M_3M_3M_4M_4\ldots m_{2911}m_{2911}$ or are highly similar to this marker profile across the 2911 SNP loci. However, the probability of such a perfect or near-perfect genotype at many loci is low, and this was evidenced by the large difference between the expected gains at the selection limit (when a line has the favorable SNP allele at each locus) and the predicted performance of the best line found in an A/B population. In the P1/P2 cross, for example, the expected gain at the selection limit was 0.81 Mg $ha^{-1}$, whereas the gain of the best line identified via the GCA model was only 0.42 Mg $ha^{-1}$. The low probability (due to linkage and the large number of loci) of the perfect

marker profile in a biparental cross therefore leads to the minimal loss in genetic diversity when one generation of genomewide selection is conducted in a biparental cross.

The genetic similarity when selection was for the retrospective index followed the same trends as when selection was for grain yield or moisture. The differences among $S_{0.05}$ values for grain yield, moisture, and the retrospective index were $\leq 0.01$ regardless of the selection procedure used (Table 14). Multiple-trait selection, at least for the two most important traits in maize, therefore does not lead to a greater retention of genetic diversity within a biparental cross.

Even though the GCA model and A/B model utilized different training population designs to predict the performance of the A/B population, the two models did not lead to significant differences in genetic similarity among the selected lines (Table 14). This result was observed for all of the traits and for all percentages of the top $F_3$ lines selected. The GCA model utilized multiple A/* and */B populations as the training population. For example, the P1/P2 test population had 16 P1/* and 9 */P2 crosses as the training population. We were unable to measure the genetic diversity in the pooled A/* and */B crosses because the populations were genotyped with different sets of markers. Nevertheless, we surmise that the training population as a whole was more diverse with the GCA model than with the A/B model, which utilized only one cross (A/B itself) as the training population. The lack of significant differences in genetic similarity between the GCA model and A/B model indicated that a greater genetic diversity in the training population does not improve the retention of genetic diversity among the selected lines.

*Influence of Prediction Accuracy and Response to Selection on Genetic Similarity of Selected Lines*

Compared with phenotypic selection, genomewide selection (via the GCA model and A/B model) had a lower prediction accuracy and a higher genetic similarity among the selected lines (Table 18). Furthermore, none of the correlations between the prediction accuracy and $S_{0.05}$ or $S_{0.10}$ values was significant for phenotypic selection, the GCA model, and the A/B model. The response to selection for the top 10% also was not significantly correlated to $S_{0.10}$ for phenotypic selection, the GCA model, and the A/B model. The retrospective index was the only trait with a significantly higher R with phenotypic selection than with the A/B model and GCA model. However, the correlation between R and $S_{0.10}$ for the retrospective index was not significant (0.10 for phenotypic selection, 0.11 for the A/B model, and 0.15 for the GCA model). The correlation between $r_{MP}$ and $S_{0.10}$ for the retrospective index was also not significant (0.17 for phenotypic selection, 0.22 for the A/B model, and 0.02 for the GCA model). Overall, the prediction accuracy and response to selection had no influence on the genetic similarity of the selected lines for all methods of selection.

*Implications for Long-Term Genomewide Selection*

Genetic diversity is needed to sustain long-term gains from selection. Our results support concerns that the loss of genetic diversity in breeding populations may be greater with genomewide selection than with phenotypic selection. However, the loss of genetic diversity with genomewide selection is small: the mean genetic similarity among the selected lines ($S_{0.05}$ = 0.57) was much lower than the maximum genetic similarity between two random lines (0.71) or than the similarity among the same proportion of lines that were

most similar (0.68). We recommend genomewide selection of more than 25% of the individuals in the population if the desire is to limit the loss in genetic diversity to a level comparable with phenotypic selection. On the other hand, such nonstringent selection would reduce the response to genomewide selection.

A breeder aims for genetic gain from selection both within and across populations. Therefore, a breeder should also maintain genetic diversity both within and across populations. In this study, we focused only on selection within a population because differences in the sets of markers did not allow us to measure the genetic similarity among the pool of lines selected across all 27 A/B populations. Newly developed lines are used as parents of new breeding populations; if genomewide selection leads to a loss in genetic diversity within biparental crosses, this loss in diversity within crosses could translate to a loss of diversity among crosses. We speculate that the minimal loss due to genomewide selection within a population would lead to only a minimal loss, if any, in genetic diversity across populations. However, if a breeder finds that genomewide selection within biparental populations is somehow leading to a loss of genetic diversity across populations, the breeder may place additional weights on low-frequency favorable alleles to retain genetic diversity (Dekkers and van Arendonk, 1998; Li et al., 2008; Goddard, 2009). These alleles can be identified based on the frequency of SNP alleles across the parents of all of the A/B test populations.

Table 13: Test and training populations for phenotypic selection, and genomewide selection via the A/B model and genetic combining ability (GCA) model in maize biparental crosses.

| | Test populations | | | | | GCA model | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Training populations | | | |
| Group[†] | A/B population | Tester | $N$[‡] | Locations | Genetic similarity[§] | A/* | */B | $N_x$[¶] | $N_{GCA}$[#] |
| 1 | P1/P2 | T1 | 152 | 7 | 0.51 (0.28-0.75) | 16 | 9 | 25 | 4066 |
| 1 | P3/P4 | T1 | 164 | 8 | 0.52 (0.36-0.66) | 6 | 11 | 17 | 2940 |
| 1 | P4/P5 | T1 | 177 | 6 | 0.51 (0.23-0.71) | 12 | 5 | 17 | 3175 |
| 1 | P6/P7 | T1 | 183 | 12 | 0.51 (0.30-0.70) | 11 | 3 | 14 | 2705 |
| 1 | P3/P8 | T1 | 181 | 7 | 0.51 (0.33-0.71) | 5 | 4 | 9 | 1493 |
| 1 | P1/P9 | T2 | 174 | 5 | 0.53 (0.30-0.77) | 7 | 4 | 11 | 1558 |
| 1 | P5/P8 | T1 | 148 | 6 | 0.51 (0.32-0.69) | 8 | 4 | 12 | 1623 |
| 1 | P9/P10 | T2 | 152 | 8 | 0.52 (0.35-0.67) | 5 | 5 | 10 | 1794 |
| 1 | P11/P12 | T1 | 182 | 8 | 0.51 (0.36-0.67) | 2 | 5 | 7 | 935 |
| 1 | P13/P14 | T3 | 178 | 8 | 0.54 (0.38-0.74) | 4 | 3 | 7 | 1256 |
| 1 | P2/P15 | T3 | 160 | 5 | 0.51 (0.34-0.68) | 5 | 3 | 8 | 982 |
| 1 | P16/P13 | T3 | 178 | 7 | 0.53 (0.34-0.76) | 4 | 2 | 6 | 1058 |
| 1 | P17/P18 | T1 | 185 | 7 | 0.52 (0.37-0.68) | 1 | 3 | 4 | 524 |
| 1 | P19/P20 | T4 | 186 | 5 | 0.51 (0.34-0.73) | 2 | 2 | 4 | 676 |
| 2 | P21/P22 | T5 | 173 | 8 | 0.52 (0.33-0.73) | 14 | 12 | 26 | 4357 |
| 2 | P23/P24 | T6 | 174 | 7 | 0.51 (0.29-0.74) | 9 | 7 | 16 | 2860 |
| 2 | P25/P22 | T5 | 169 | 8 | 0.51 (0.34-0.73) | 13 | 4 | 17 | 2912 |
| 2 | P26/P27 | T6 | 184 | 6 | 0.51 (0.33-0.73) | 10 | 6 | 16 | 2587 |
| 2 | P23/P25 | T5 | 168 | 7 | 0.50 (0.34-0.68) | 4 | 12 | 16 | 2558 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 2 | P24/P26 | T6 | 183 | 6 | 0.58 (0.41-0.75) | 7 | 10 | 17 | 2863 |
| 2 | P28/P27 | T6 | 180 | 8 | 0.53 (0.27-0.75) | 6 | 3 | 9 | 1510 |
| 2 | P29/P27 | T6 | 175 | 7 | 0.51 (0.31-0.69) | 4 | 6 | 10 | 1698 |
| 2 | P29/P30 | T6 | 183 | 5 | 0.51 (0.33-0.68) | 4 | 6 | 10 | 1801 |
| 2 | P31/P32 | T7 | 170 | 8 | 0.51 (0.34-0.69) | 2 | 5 | 7 | 1251 |
| 2 | P33/P34 | T8 | 181 | 7 | 0.51 (0.31-0.72) | 2 | 2 | 4 | 715 |
| 2 | P35/P36 | T9 | 139 | 4 | 0.51 (0.33-0.69) | 3 | 2 | 5 | 619 |
| 2 | P37/P38 | T10 | 183 | 5 | 0.51 (0.36-0.70) | 2 | 2 | 4 | 532 |

[†]Heterotic group.

[‡]*N*, number of $F_3$ lines in the A/B test population.

[§]Mean similarity, with minimum and maximum similarity in parentheses.

[¶]$N_X$, number of biparental crosses in the training population for the GCA model.

[#]$N_{GCA}$, number of $F_3$ lines in the training population for the GCA model.

Table 14: Genetic similarity before and after phenotypic selection and genomewide selection via the A/B model and general combining ability (GCA) model across 27 biparental maize populations.

| | | Best % selected for grain yield | | | | Best % selected for moisture | | | | Best % selected for index | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Method | No selection | 5 | 10 | 25 | 50 | 5 | 10 | 25 | 50 | 5 | 10 | 25 | 50 |
| Phenotypic selection | 0.52 (0.50, 0.58) | 0.53$^{b\dagger}$ (0.51, 0.58) | 0.52$^{b}$ (0.50, 0.58) | 0.52$^{b}$ (0.51, 0.58) | 0.52$^{a}$ (0.50, 0.58) | 0.53$^{b}$ (0.50, 0.59) | 0.53$^{b}$ (0.50, 0.59) | 0.52$^{b}$ (0.50, 0.58) | 0.52$^{a}$ (0.50, 0.58) | 0.53$^{b}$ (0.51, 0.58) | 0.52$^{b}$ (0.51, 0.58) | 0.52$^{b}$ (0.50, 0.58) | 0.52$^{a}$ (0.50, 0.58) |
| A/B model | 0.52 (0.50, 0.58) | 0.57$^{a}$ (0.53, 0.63) | 0.55$^{a}$ (0.53, 0.62) | 0.54$^{a}$ (0.52, 0.61) | 0.52$^{a}$ (0.51, 0.59) | 0.56$^{a}$ (0.54, 0.62) | 0.55$^{a}$ (0.52, 0.61) | 0.53$^{a}$ (0.51, 0.56) | 0.52$^{a}$ (0.51, 0.59) | 0.56$^{a}$ (0.51, 0.61) | 0.55$^{a}$ (0.52, 0.61) | 0.54$^{a}$ (0.51, 0.60) | 0.52$^{a}$ (0.51, 0.59) |
| GCA model | 0.52 (0.50, 0.58) | 0.57$^{a}$ (0.53, 0.64) | 0.55$^{a}$ (0.52, 0.62) | 0.54$^{a}$ (0.51, 0.60) | 0.52$^{a}$ (0.51, 0.59) | 0.57$^{a}$ (0.53, 0.62) | 0.55$^{a}$ (0.53, 0.61) | 0.53$^{a}$ (0.51, 0.60) | 0.52$^{a}$ (0.51, 0.59) | 0.56$^{a}$ (0.52, 0.62) | 0.55$^{a}$ (0.52, 0.61) | 0.53$^{a}$ (0.51, 0.59) | 0.52$^{a}$ (0.50, 0.59) |
| LSD | | 0.011 | 0.011 | 0.009 | 0.009 | 0.010 | 0.010 | 0.010 | 0.008 | 0.012 | 0.010 | 0.009 | 0.009 |

$^{\dagger}$Within a column, estimates with a common letter were not significantly different ($p$=0.05).

Table 15: Mean genetic similarity (maximum similarity in parentheses) when phenotypic selection, the A/B model and the general combining ability (GCA) model are used to select the best 5, 10, 25 and 50% of the population for maize grain yield.

| | Phenotypic selection of the top % | | | | A/B model to select the top % | | | | GCA model to select the top % | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 5 | 10 | 25 | 50 | 5 | 10 | 25 | 50 | 5 | 10 | 25 | 50 |
| P1/P2 | 0.53 (0.65) | 0.52 (0.65) | 0.51 (0.67) | 0.51 (0.75) | 0.59 (0.67) | 0.57 (0.67) | 0.54 (0.67) | 0.52 (0.69) | 0.59 (0.69) | 0.57 (0.69) | 0.54 (0.75) | 0.52 (0.75) |
| P3/P4 | 0.52 (0.60) | 0.50 (0.60) | 0.51 (0.62) | 0.50 (0.65) | 0.57 (0.65) | 0.55 (0.65) | 0.53 (0.65) | 0.51 (0.65) | 0.55 (0.61) | 0.53 (0.62) | 0.52 (0.65) | 0.51 (0.66) |
| P4/P5 | 0.51 (0.60) | 0.51 (0.62) | 0.51 (0.65) | 0.51 (0.66) | 0.55 (0.62) | 0.53 (0.62) | 0.52 (0.62) | 0.51 (0.65) | 0.56 (0.63) | 0.53 (0.64) | 0.52 (0.66) | 0.51 (0.66) |
| P6/P7 | 0.51 (0.61) | 0.52 (0.63) | 0.51 (0.65) | 0.51 (0.65) | 0.55 (0.64) | 0.54 (0.64) | 0.53 (0.66) | 0.52 (0.67) | 0.55 (0.69) | 0.54 (0.69) | 0.52 (0.70) | 0.51 (0.70) |
| P3/P8 | 0.51 (0.58) | 0.52 (0.66) | 0.52 (0.66) | 0.51 (0.68) | 0.56 (0.70) | 0.56 (0.70) | 0.54 (0.70) | 0.52 (0.71) | 0.54 (0.59) | 0.53 (0.64) | 0.52 (0.67) | 0.51 (0.71) |
| P1/ P9 | 0.53 (0.62) | 0.54 (0.70) | 0.53 (0.70) | 0.52 (0.70) | 0.61 (0.69) | 0.57 (0.70) | 0.56 (0.77) | 0.54 (0.77) | 0.60 (0.69) | 0.57 (0.71) | 0.55 (0.71) | 0.54 (0.77) |
| P5/P8 | 0.57 (0.65) | 0.52 (0.66) | 0.52 (0.68) | 0.51 (0.68) | 0.58 (0.66) | 0.56 (0.66) | 0.54 (0.68) | 0.52 (0.68) | 0.59 (0.66) | 0.57 (0.68) | 0.54 (0.68) | 0.52 (0.68) |
| P9/P10 | 0.51 (0.59) | 0.51 (0.60) | 0.52 (0.62) | 0.51 (0.66) | 0.55 (0.61) | 0.54 (0.65) | 0.53 (0.65) | 0.52 (0.65) | 0.56 (0.64) | 0.55 (0.64) | 0.53 (0.64) | 0.52 (0.67) |
| P11/P12 | 0.51 (0.63) | 0.51 (0.63) | 0.51 (0.63) | 0.51 (0.63) | 0.55 (0.65) | 0.53 (0.65) | 0.52 (0.65) | 0.52 (0.66) | 0.56 (0.63) | 0.54 (0.64) | 0.53 (0.66) | 0.52 (0.66) |
| P13/P14 | 0.56 (0.69) | 0.56 (0.69) | 0.55 (0.69) | 0.55 (0.71) | 0.59 (0.70) | 0.57 (0.71) | 0.56 (0.71) | 0.55 (0.71) | 0.59 (0.64) | 0.57 (0.66) | 0.56 (0.68) | 0.55 (0.69) |
| P2/P15 | 0.51 (0.61) | 0.52 (0.62) | 0.52 (0.64) | 0.51 (0.67) | 0.57 (0.66) | 0.55 (0.66) | 0.53 (0.67) | 0.52 (0.67) | 0.54 (0.64) | 0.54 (0.64) | 0.52 (0.64) | 0.52 (0.67) |
| P16/P13 | 0.55 (0.64) | 0.55 (0.68) | 0.54 (0.70) | 0.54 (0.76) | 0.58 (0.66) | 0.57 (0.71) | 0.56 (0.73) | 0.55 (0.76) | 0.58 (0.73) | 0.58 (0.73) | 0.56 (0.73) | 0.54 (0.76) |
| P17/P18 | 0.53 (0.62) | 0.53 (0.64) | 0.52 (0.67) | 0.52 (0.68) | 0.56 (0.64) | 0.54 (0.65) | 0.53 (0.65) | 0.52 (0.67) | 0.56 (0.63) | 0.54 (0.63) | 0.53 (0.67) | 0.52 (0.68) |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P19/P20 | 0.51 (0.60) | 0.51 (0.60) | 0.51 (0.63) | 0.51 (0.65) | 0.54 (0.62) | 0.53 (0.62) | 0.52 (0.67) | 0.51 (0.67) | 0.53 (0.62) | 0.52 (0.62) | 0.51 (0.62) | 0.51 (0.67) |
| P21/P22 | 0.54 (0.66) | 0.52 (0.67) | 0.52 (0.69) | 0.52 (0.70) | 0.57 (0.68) | 0.56 (0.68) | 0.54 (0.70) | 0.53 (0.70) | 0.58 (0.68) | 0.56 (0.68) | 0.54 (0.70) | 0.52 (0.70) |
| P23/P24 | 0.51 (0.61) | 0.51 (0.65) | 0.51 (0.70) | 0.51 (0.73) | 0.58 (0.64) | 0.53 (0.65) | 0.52 (0.71) | 0.51 (0.71) | 0.59 (0.68) | 0.59 (0.70) | 0.54 (0.73) | 0.53 (0.73) |
| P25/P22 | 0.51 (0.58) | 0.51 (0.61) | 0.52 (0.65) | 0.51 (0.69) | 0.56 (0.65) | 0.54 (0.65) | 0.53 (0.66) | 0.52 (0.66) | 0.55 (0.64) | 0.55 (0.65) | 0.53 (0.66) | 0.52 (0.66) |
| P26/P27 | 0.52 (0.61) | 0.52 (0.68) | 0.52 (0.68) | 0.52 (0.71) | 0.56 (0.65) | 0.56 (0.68) | 0.54 (0.70) | 0.52 (0.71) | 0.58 (0.68) | 0.57 (0.68) | 0.55 (0.71) | 0.53 (0.71) |
| P23/P25 | 0.51 (0.59) | 0.51 (0.60) | 0.51 (0.65) | 0.51 (0.65) | 0.54 (0.63) | 0.53 (0.65) | 0.52 (0.65) | 0.51 (0.68) | 0.56 (0.65) | 0.54 (0.65) | 0.52 (0.65) | 0.51 (0.65) |
| P24/P26 | 0.58 (0.68) | 0.58 (0.68) | 0.58 (0.75) | 0.58 (0.75) | 0.63 (0.72) | 0.62 (0.72) | 0.60 (0.72) | 0.59 (0.72) | 0.63 (0.69) | 0.62 (0.72) | 0.60 (0.72) | 0.59 (0.72) |
| P28/P27 | 0.53 (0.62) | 0.54 (0.66) | 0.54 (0.72) | 0.54 (0.72) | 0.58 (0.71) | 0.57 (0.71) | 0.56 (0.75) | 0.55 (0.75) | 0.61 (0.69) | 0.58 (0.70) | 0.56 (0.75) | 0.55 (0.75) |
| P29/P27 | 0.51 (0.64) | 0.51 (0.64) | 0.51 (0.64) | 0.51 (0.68) | 0.53 (0.67) | 0.54 (0.67) | 0.52 (0.68) | 0.51 (0.68) | 0.54 (0.62) | 0.54 (0.68) | 0.53 (0.69) | 0.52 (0.69) |
| P29/P30 | 0.53 (0.65) | 0.52 (0.65) | 0.51 (0.65) | 0.51 (0.67) | 0.55 (0.65) | 0.54 (0.65) | 0.53 (0.65) | 0.52 (0.65) | 0.55 (0.60) | 0.52 (0.61) | 0.52 (0.67) | 0.51 (0.67) |
| P33/P34 | 0.50 (0.62) | 0.50 (0.62) | 0.51 (0.65) | 0.51 (0.66) | 0.56 (0.66) | 0.54 (0.66) | 0.53 (0.68) | 0.52 (0.68) | 0.55 (0.68) | 0.54 (0.68) | 0.52 (0.68) | 0.51 (0.68) |
| P35/P36 | 0.51 (0.60) | 0.51 (0.66) | 0.51 (0.70) | 0.51 (0.70) | 0.55 (0.62) | 0.54 (0.71) | 0.53 (0.71) | 0.52 (0.72) | 0.54 (0.65) | 0.53 (0.65) | 0.52 (0.69) | 0.51 (0.69) |
| P37/P38 | 0.51 (0.68) | 0.52 (0.68) | 0.52 (0.68) | 0.51 (0.68) | 0.55 (0.68) | 0.54 (0.68) | 0.53 (0.68) | 0.52 (0.69) | 0.54 (0.65) | 0.53 (0.65) | 0.52 (0.65) | 0.51 (0.66) |
| P41/P42 | 0.53 (0.60) | 0.52 (0.63) | 0.51 (0.63) | 0.51 (0.65) | 0.56 (0.64) | 0.53 (0.64) | 0.53 (0.64) | 0.52 (0.64) | 0.55 (0.63) | 0.54 (0.63) | 0.52 (0.66) | 0.52 (0.69) |

Table 16: Mean genetic similarity (maximum similarity in parentheses) when phenotypic selection, the A/B model and the general combining ability (GCA) model are used to select the best 5, 10, 25 and 50% of the population for maize moisture.

| | Phenotypic selection of the top % | | | | A/B model to select the top % | | | | GCA model to select the top % | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 5 | 10 | 25 | 50 | 5 | 10 | 25 | 50 | 5 | 10 | 25 | 50 |
| P1/P2 | 0.51 (0.61) | 0.52 (0.64) | 0.51 (0.67) | 0.51 (0.69) | 0.57 (0.68) | 0.55 (0.68) | 0.53 (0.68) | 0.51 (0.69) | 0.55 (0.68) | 0.54 (0.68) | 0.52 (0.69) | 0.51 (0.75) |
| P3/P4 | 0.51 (0.60) | 0.50 (0.65) | 0.50 (0.65) | 0.50 (0.65) | 0.55 (0.65) | 0.53 (0.65) | 0.51 (0.65) | 0.51 (0.65) | 0.53 (0.62) | 0.53 (0.63) | 0.52 (0.65) | 0.51 (0.65) |
| P4/P5 | 0.51 (0.59) | 0.52 (0.60) | 0.52 (0.62) | 0.51 (0.65) | 0.55 (0.61) | 0.53 (0.61) | 0.52 (0.64) | 0.51 (0.65) | 0.55 (0.61) | 0.54 (0.62) | 0.53 (0.65) | 0.52 (0.65) |
| P6/P7 | 0.52 (0.63) | 0.51 (0.63) | 0.51 (0.67) | 0.51 (0.67) | 0.55 (0.61) | 0.53 (0.63) | 0.52 (0.64) | 0.51 (0.67) | 0.56 (0.62) | 0.54 (0.63) | 0.51 (0.64) | 0.52 (0.66) |
| P3/P8 | 0.50 (0.59) | 0.51 (0.60) | 0.51 (0.66) | 0.51 (0.67) | 0.56 (0.63) | 0.53 (0.63) | 0.52 (0.64) | 0.51 (0.67) | 0.54 (0.63) | 0.53 (0.63) | 0.52 (0.63) | 0.51 (0.67) |
| P1/ P9 | 0.56 (0.65) | 0.54 (0.66) | 0.53 (0.69) | 0.52 (0.77) | 0.58 (0.70) | 0.56 (0.72) | 0.55 (0.72) | 0.53 (0.77) | 0.57 (0.68) | 0.57 (0.77) | 0.55 (0.77) | 0.53 (0.77) |
| P5/P8 | 0.53 (0.62) | 0.52 (0.66) | 0.52 (0.69) | 0.51 (0.69) | 0.59 (0.69) | 0.55 (0.69) | 0.53 (0.69) | 0.52 (0.69) | 0.59 (0.67) | 0.56 (0.68) | 0.53 (0.69) | 0.52 (0.69) |
| P9/P10 | 0.54 (0.60) | 0.54 (0.64) | 0.53 (0.64) | 0.52 (0.67) | 0.56 (0.63) | 0.53 (0.64) | 0.53 (0.64) | 0.52 (0.65) | 0.55 (0.61) | 0.54 (0.65) | 0.53 (0.65) | 0.52 (0.66) |
| P11/P12 | 0.51 (0.60) | 0.52 (0.61) | 0.52 (0.64) | 0.51 (0.66) | 0.54 (0.60) | 0.54 (0.62) | 0.52 (0.66) | 0.51 (0.67) | 0.54 (0.63) | 0.53 (0.66) | 0.52 (0.66) | 0.51 (0.66) |
| P13/P14 | 0.56 (0.71) | 0.56 (0.71) | 0.55 (0.74) | 0.55 (0.74) | 0.61 (0.71) | 0.59 (0.71) | 0.56 (0.71) | 0.55 (0.71) | 0.62 (0.74) | 0.61 (0.74) | 0.58 (0.74) | 0.56 (0.74) |
| P2/P15 | 0.50 (0.62) | 0.51 (0.65) | 0.51 (0.67) | 0.51 (0.68) | 0.55 (0.64) | 0.52 (0.64) | 0.51 (0.68) | 0.51 (0.68) | 0.54 (0.63) | 0.53 (0.63) | 0.51 (0.68) | 0.51 (0.68) |
| P16/P13 | 0.55 (0.64) | 0.54 (0.70) | 0.54 (0.74) | 0.53 (0.74) | 0.58 (0.70) | 0.56 (0.70) | 0.55 (0.74) | 0.54 (0.74) | 0.59 (0.70) | 0.57 (0.70) | 0.55 (0.71) | 0.54 (0.74) |
| P17/P18 | 0.55 (0.68) | 0.55 (0.68) | 0.54 (0.68) | 0.52 (0.68) | 0.57 (0.65) | 0.56 (0.68) | 0.55 (0.68) | 0.53 (0.68) | 0.58 (0.65) | 0.54 (0.68) | 0.53 (0.68) | 0.52 (0.68) |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P19/P20 | 0.52 (0.60) | 0.52 (0.66) | 0.51 (0.66) | 0.51 (0.66) | 0.55 (0.63) | 0.53 (0.63) | 0.52 (0.64) | 0.52 (0.67) | 0.55 (0.62) | 0.53 (0.62) | 0.52 (0.66) | 0.51 (0.66) |
| P21/P22 | 0.51 (0.62) | 0.53 (0.67) | 0.53 (0.73) | 0.52 (0.73) | 0.57 (0.66) | 0.55 (0.66) | 0.53 (0.68) | 0.52 (0.73) | 0.57 (0.66) | 0.55 (0.67) | 0.54 (0.68) | 0.52 (0.68) |
| P23/P24 | 0.52 (0.63) | 0.51 (0.64) | 0.52 (0.68) | 0.51 (0.72) | 0.58 (0.65) | 0.54 (0.67) | 0.54 (0.68) | 0.52 (0.70) | 0.60 (0.68) | 0.56 (0.68) | 0.54 (0.70) | 0.53 (0.73) |
| P25/P22 | 0.53 (0.62) | 0.53 (0.63) | 0.51 (0.63) | 0.51 (0.66) | 0.57 (0.63) | 0.54 (0.66) | 0.53 (0.66) | 0.52 (0.66) | 0.57 (0.66) | 0.54 (0.66) | 0.53 (0.66) | 0.52 (0.73) |
| P26/P27 | 0.52 (0.64) | 0.53 (0.68) | 0.52 (0.70) | 0.52 (0.70) | 0.57 (0.68) | 0.54 (0.68) | 0.53 (0.70) | 0.52 (0.70) | 0.58 (0.68) | 0.57 (0.68) | 0.54 (0.69) | 0.52 (0.70) |
| P23/P25 | 0.52 (0.62) | 0.51 (0.62) | 0.51 (0.64) | 0.51 (0.67) | 0.56 (0.61) | 0.54 (0.63) | 0.52 (0.64) | 0.51 (0.67) | 0.55 (0.61) | 0.54 (0.64) | 0.52 (0.64) | 0.51 (0.67) |
| P24/P26 | 0.59 (0.69) | 0.59 (0.70) | 0.58 (0.70) | 0.58 (0.72) | 0.62 (0.70) | 0.61 (0.70) | 0.60 (0.72) | 0.58 (0.72) | 0.61 (0.69) | 0.61 (0.72) | 0.60 (0.72) | 0.58 (0.75) |
| P28/P27 | 0.54 (0.73) | 0.55 (0.73) | 0.55 (0.73) | 0.54 (0.73) | 0.58 (0.73) | 0.57 (0.73) | 0.56 (0.73) | 0.54 (0.73) | 0.58 (0.73) | 0.56 (0.73) | 0.54 (0.73) | 0.53 (0.73) |
| P29/P27 | 0.52 (0.63) | 0.52 (0.63) | 0.52 (0.65) | 0.51 (0.69) | 0.54 (0.61) | 0.53 (0.69) | 0.52 (0.69) | 0.52 (0.69) | 0.53 (0.61) | 0.54 (0.64) | 0.53 (0.69) | 0.52 (0.69) |
| P29/P30 | 0.54 (0.63) | 0.53 (0.63) | 0.52 (0.66) | 0.52 (0.67) | 0.57 (0.65) | 0.55 (0.65) | 0.53 (0.66) | 0.52 (0.68) | 0.57 (0.65) | 0.54 (0.65) | 0.52 (0.65) | 0.52 (0.67) |
| P33/P34 | 0.51 (0.60) | 0.52 (0.64) | 0.51 (0.69) | 0.51 (0.69) | 0.55 (0.62) | 0.55 (0.69) | 0.53 (0.69) | 0.52 (0.69) | 0.56 (0.69) | 0.55 (0.69) | 0.53 (0.69) | 0.52 (0.69) |
| P35/P36 | 0.51 (0.59) | 0.51 (0.62) | 0.51 (0.69) | 0.51 (0.72) | 0.56 (0.63) | 0.55 (0.70) | 0.54 (0.72) | 0.52 (0.72) | 0.55 (0.67) | 0.55 (0.69) | 0.53 (0.70) | 0.52 (0.70) |
| P37/P38 | 0.52 (0.61) | 0.52 (0.62) | 0.52 (0.65) | 0.51 (0.67) | 0.55 (0.62) | 0.55 (0.65) | 0.54 (0.66) | 0.52 (0.67) | 0.55 (0.62) | 0.53 (0.65) | 0.52 (0.66) | 0.51 (0.69) |
| P41/P42 | 0.54 (0.62) | 0.53 (0.66) | 0.52 (0.66) | 0.51 (0.66) | 0.56 (0.66) | 0.54 (0.66) | 0.53 (0.66) | 0.52 (0.66) | 0.56 (0.62) | 0.54 (0.63) | 0.53 (0.66) | 0.52 (0.66) |

Table 17: Mean genetic similarity (maximum similarity in parentheses) when phenotypic selection, the A/B model and the general combining ability (GCA) model are used to select the best 5, 10, 25 and 50% of the population for the index.

| | Phenotypic selection of the top % | | | | A/B model to select the top % | | | | GCA model to select the top % | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 5 | 10 | 25 | 50 | 5 | 10 | 25 | 50 | 5 | 10 | 25 | 50 |
| P1/P2 | 0.54 (0.65) | 0.52 (0.65) | 0.51 (0.67) | 0.51 (0.69) | 0.59 (0.66) | 0.56 (0.67) | 0.54 (0.69) | 0.52 (0.69) | 0.58 (0.66) | 0.57 (0.69) | 0.55 (0.75) | 0.52 (0.75) |
| P3/P4 | 0.52 (0.60) | 0.51 (0.62) | 0.50 (0.65) | 0.50 (0.65) | 0.53 (0.63) | 0.53 (0.63) | 0.53 (0.65) | 0.52 (0.65) | 0.55 (0.65) | 0.53 (0.65) | 0.51 (0.65) | 0.50 (0.66) |
| P4/P5 | 0.51 (0.57) | 0.51 (0.60) | 0.50 (0.65) | 0.50 (0.66) | 0.51 (0.59) | 0.52 (0.64) | 0.52 (0.64) | 0.51 (0.66) | 0.56 (0.64) | 0.54 (0.64) | 0.53 (0.64) | 0.52 (0.66) |
| P6/P7 | 0.52 (0.61) | 0.51 (0.61) | 0.51 (0.65) | 0.51 (0.65) | 0.54 (0.63) | 0.53 (0.63) | 0.52 (0.66) | 0.51 (0.66) | 0.53 (0.63) | 0.53 (0.64) | 0.52 (0.65) | 0.51 (0.65) |
| P3/P8 | 0.52 (0.58) | 0.52 (0.66) | 0.51 (0.67) | 0.51 (0.68) | 0.53 (0.63) | 0.52 (0.63) | 0.52 (0.65) | 0.51 (0.71) | 0.54 (0.62) | 0.53 (0.62) | 0.52 (0.63) | 0.51 (0.71) |
| P1/ P9 | 0.53 (0.60) | 0.53 (0.70) | 0.53 (0.70) | 0.52 (0.72) | 0.61 (0.70) | 0.58 (0.70) | 0.56 (0.77) | 0.54 (0.77) | 0.60 (0.71) | 0.59 (0.71) | 0.56 (0.71) | 0.54 (0.77) |
| P5/P8 | 0.57 (0.65) | 0.53 (0.66) | 0.52 (0.67) | 0.51 (0.68) | 0.58 (0.66) | 0.57 (0.66) | 0.54 (0.68) | 0.52 (0.69) | 0.58 (0.66) | 0.56 (0.67) | 0.54 (0.68) | 0.52 (0.68) |
| P9/P10 | 0.54 (0.61) | 0.52 (0.61) | 0.52 (0.64) | 0.52 (0.64) | 0.55 (0.62) | 0.54 (0.64) | 0.53 (0.64) | 0.52 (0.65) | 0.54 (0.61) | 0.53 (0.61) | 0.53 (0.64) | 0.52 (0.66) |
| P11/P12 | 0.52 (0.57) | 0.52 (0.63) | 0.51 (0.63) | 0.51 (0.66) | 0.54 (0.65) | 0.53 (0.65) | 0.52 (0.67) | 0.51 (0.67) | 0.54 (0.63) | 0.54 (0.63) | 0.53 (0.67) | 0.52 (0.67) |
| P13/P14 | 0.58 (0.69) | 0.56 (0.69) | 0.55 (0.69) | 0.55 (0.71) | 0.60 (0.70) | 0.58 (0.71) | 0.56 (0.71) | 0.55 (0.61) | 0.58 (0.65) | 0.56 (0.65) | 0.56 (0.67) | 0.55 (0.71) |
| P2/P15 | 0.52 (0.59) | 0.52 (0.64) | 0.51 (0.65) | 0.51 (0.67) | 0.58 (0.66) | 0.55 (0.67) | 0.53 (0.67) | 0.52 (0.67) | 0.52 (0.60) | 0.52 (0.62) | 0.51 (0.64) | 0.51 (0.65) |
| P16/P13 | 0.56 (0.63) | 0.55 (0.68) | 0.54 (0.68) | 0.54 (0.76) | 0.59 (0.66) | 0.56 (0.67) | 0.55 (0.73) | 0.54 (0.73) | 0.59 (0.73) | 0.57 (0.73) | 0.55 (0.73) | 0.54 (0.76) |
| P17/P18 | 0.54 (0.63) | 0.53 (0.67) | 0.52 (0.68) | 0.52 (0.68) | 0.56 (0.67) | 0.56 (0.67) | 0.54 (0.68) | 0.53 (0.68) | 0.56 (0.64) | 0.56 (0.68) | 0.54 (0.68) | 0.52 (0.68) |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P19/P20 | 0.51 (0.59) | 0.51 (0.60) | 0.51 (0.63) | 0.51 (0.67) | 0.55 (0.63) | 0.54 (0.65) | 0.52 (0.67) | 0.51 (0.67) | 0.54 (0.62) | 0.53 (0.62) | 0.52 (0.62) | 0.51 (0.67) |
| P21/P22 | 0.54 (0.66) | 0.52 (0.66) | 0.52 (0.69) | 0.52 (0.73) | 0.57 (0.69) | 0.56 (0.69) | 0.54 (0.69) | 0.53 (0.69) | 0.57 (0.67) | 0.55 (0.68) | 0.54 (0.68) | 0.52 (0.70) |
| P23/P24 | 0.52 (0.65) | 0.51 (0.65) | 0.51 (0.70) | 0.51 (0.73) | 0.55 (0.65) | 0.55 (0.67) | 0.53 (0.70) | 0.52 (0.70) | 0.60 (0.70) | 0.59 (0.73) | 0.55 (0.73) | 0.53 (0.73) |
| P25/P22 | 0.51 (0.59) | 0.51 (0.61) | 0.52 (0.64) | 0.52 (0.65) | 0.57 (0.64) | 0.55 (0.64) | 0.53 (0.66) | 0.52 (0.66) | 0.56 (0.66) | 0.55 (0.66) | 0.53 (0.66) | 0.52 (0.66) |
| P26/P27 | 0.52 (0.62) | 0.52 (0.63) | 0.52 (0.68) | 0.51 (0.69) | 0.56 (0.64) | 0.55 (0.67) | 0.53 (0.68) | 0.52 (0.71) | 0.59 (0.66) | 0.56 (0.68) | 0.54 (0.71) | 0.52 (0.71) |
| P23/P25 | 0.51 (0.58) | 0.51 (0.61) | 0.51 (0.62) | 0.51 (0.65) | 0.53 (0.61) | 0.52 (0.65) | 0.51 (0.65) | 0.51 (0.68) | 0.55 (0.61) | 0.53 (0.64) | 0.52 (0.65) | 0.51 (0.67) |
| P24/P26 | 0.58 (0.68) | 0.58 (0.68) | 0.58 (0.75) | 0.58 (0.75) | 0.61 (0.70) | 0.61 (0.70) | 0.60 (0.72) | 0.59 (0.72) | 0.62 (0.71) | 0.61 (0.71) | 0.59 (0.75) | 0.59 (0.75) |
| P28/P27 | 0.55 (0.63) | 0.55 (0.67) | 0.54 (0.71) | 0.54 (0.73) | 0.58 (0.73) | 0.57 (0.73) | 0.56 (0.73) | 0.55 (0.73) | 0.61 (0.73) | 0.58 (0.73) | 0.55 (0.73) | 0.54 (0.73) |
| P29/P27 | 0.52 (0.60) | 0.51 (0.63) | 0.51 (0.64) | 0.51 (0.69) | 0.54 (0.62) | 0.53 (0.67) | 0.52 (0.69) | 0.51 (0.69) | 0.56 (0.69) | 0.54 (0.69) | 0.52 (0.69) | 0.52 (0.69) |
| P29/P30 | 0.53 (0.65) | 0.52 (0.65) | 0.51 (0.65) | 0.51 (0.67) | 0.54 (0.61) | 0.54 (0.65) | 0.52 (0.66) | 0.52 (0.66) | 0.53 (0.59) | 0.52 (0.61) | 0.52 (0.67) | 0.51 (0.67) |
| P33/P34 | 0.53 (0.62) | 0.51 (0.62) | 0.51 (0.65) | 0.51 (0.68) | 0.54 (0.67) | 0.54 (0.67) | 0.53 (0.69) | 0.52 (0.69) | 0.54 (0.62) | 0.53 (0.63) | 0.52 (0.68) | 0.51 (0.69) |
| P35/P36 | 0.51 (0.61) | 0.51 (0.66) | 0.51 (0.66) | 0.51 (0.70) | 0.57 (0.63) | 0.56 (0.71) | 0.54 (0.72) | 0.53 (0.72) | 0.54 (0.67) | 0.53 (0.67) | 0.52 (0.69) | 0.51 (0.69) |
| P37/P38 | 0.54 (0.65) | 0.52 (0.65) | 0.52 (0.68) | 0.51 (0.68) | 0.56 (0.65) | 0.55 (0.68) | 0.53 (0.68) | 0.52 (0.68) | 0.53 (0.64) | 0.53 (0.64) | 0.52 (0.65) | 0.51 (0.69) |
| P41/P42 | 0.53 (0.62) | 0.52 (0.63) | 0.51 (0.63) | 0.51 (0.66) | 0.54 (0.63) | 0.54 (0.63) | 0.53 (0.66) | 0.52 (0.69) | 0.53 (0.62) | 0.53 (0.63) | 0.52 (0.65) | 0.52 (0.69) |

Table 18: Response to selection (R) and prediction accuracy ($r_{MP}$) for yield, moisture and index for phenotypic selection, A/B model, and general combining ability (GCA) model.

| Test Population | Grain yield | | | | | | Moisture | | | | | | Index | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | PS | A/B | GCA | PS | A/B | GCA | PS | A/B | GCA | PS | A/B | GCA | PS | A/B | GCA | PS | A/B | GCA |
| | R (Mg ha$^{-1}$) | | | $r_{MP}$ | | | R (g kg$^{-1}$) | | | $r_{MP}$ | | | R (index value) | | | $r_{MP}$ | | |
| P1/P2 | 0.45 | 0.41 | 0.31 | 0.45 | 0.21 | 0.31 | -5 | -3 | -4 | 0.42 | 0.35 | 0.48 | 0.41 | 0.22 | 0.49 | 0.42 | 0.15 | 0.30 |
| P3/P4 | 0.25 | 0.15 | 0.14 | 0.19 | 0.14 | 0.23 | -11 | -7 | -10 | 0.59 | 0.46 | 0.49 | 0.23 | 0.18 | 0.09 | 0.19 | 0.19 | 0.23 |
| P4/P5 | 0.37 | 0.19 | 0.30 | 0.31 | 0.19 | 0.27 | -7 | -5 | -5 | 0.65 | 0.56 | 0.56 | 0.36 | -0.01$^{NS\dagger}$ | -0.06 | 0.28 | 0.06 | 0.08 |
| P6/P7 | 0.33 | 0.34 | 0.23 | 0.34 | 0.37 | 0.26 | -11 | -10 | -7 | 0.72 | 0.67 | 0.51 | 0.47 | 0.39 | 0.35 | 0.37 | 0.44 | 0.41 |
| P3/P8 | 0.17 | 0.15 | 0.16 | 0.27 | 0.13 | 0.14 | -7 | -5 | -6 | 0.57 | 0.43 | 0.50 | 0.18 | 0.05 | 0.11 | 0.21 | -0.08 | 0.04 |
| P1/ P9 | 0.07 | 0.29 | 0.36 | 0.25 | 0.35 | 0.39 | -3 | -3 | -4 | 0.40 | 0.38 | 0.46 | 0.05 | 0.16 | 0.24 | 0.20 | 0.32 | 0.33 |
| P5/P8 | 0.40 | 0.45 | 0.51 | 0.27 | 0.33 | 0.32 | -2 | -2 | -2 | 0.42 | 0.36 | 0.32 | 0.28 | 0.36 | 0.42 | 0.21 | 0.27 | 0.30 |
| P9/P10 | 0.22 | 0.08 | 0.03 | 0.22 | 0.05 | -0.04 | -14 | -11 | -6 | 0.66 | 0.53 | 0.38 | 0.41 | 0.28 | 0.31 | 0.32 | 0.34 | 0.16 |
| P11/P12 | 0.18 | 0.24 | 0.39 | 0.25 | 0.19 | 0.26 | -10 | -9 | -8 | 0.74 | 0.66 | 0.63 | 0.24 | 0.11 | 0.20 | 0.19 | 0.09 | 0.16 |
| P13/P14 | 0.35 | 0.39 | 0.04 | 0.35 | 0.40 | 0.18 | -4 | -3 | -3 | 0.54 | 0.52 | 0.38 | 0.35 | 0.40 | 0.15 | 0.33 | 0.40 | 0.01$^{NS}$ |
| P2/P15 | 0.26 | 0.34 | 0.20 | 0.18 | 0.33 | 0.26 | -2 | -3 | -4 | 0.40 | 0.42 | 0.49 | 0.20 | 0.22 | 0.02 | 0.15 | 0.24 | 0.05 |
| P16/P13 | 0.36 | 0.21 | 0.13 | 0.26 | 0.27 | 0.29 | -9 | -9 | -8 | 0.62 | 0.61 | 0.60 | 0.16 | 0.02 | 0.02 | 0.15 | 0.12 | 0.23 |
| P17/P18 | 0.39 | 0.35 | 0.42 | 0.29 | 0.23 | 0.31 | -17 | -17 | -13 | 0.62 | 0.69 | 0.62 | 0.44 | 0.33 | 0.20 | 0.25 | 0.27 | 0.16 |
| P19/P20 | 0.05 | 0.25 | 0.16 | 0.13 | 0.24 | 0.22 | -6 | -3 | -4 | 0.40 | 0.27 | 0.32 | 0.00 | 0.25 | 0.14 | 0.13 | 0.22 | 0.21 |
| P21/P22 | 0.35 | 0.31 | 0.27 | 0.34 | 0.21 | 0.24 | -5 | -5 | -6 | 0.32 | 0.38 | 0.37 | 0.36 | 0.27 | 0.40 | 0.36 | 0.21 | 0.23 |
| P23/P24 | 0.15 | -0.02 | 0.04 | 0.15 | -0.05 | -0.01$^{NS}$ | -7 | -4 | -4 | 0.47 | 0.35 | 0.29 | 0.28 | -0.10 | 0.02 | 0.16 | 0.06 | 0.07 |
| P25/P22 | 0.29 | 0.24 | 0.42 | 0.32 | 0.24 | 0.29 | -9 | -7 | -7 | 0.51 | 0.36 | 0.39 | 0.35 | 0.25 | 0.24 | 0.32 | 0.23 | 0.26 |
| P26/P27 | 0.15 | 0.18 | 0.14 | 0.14 | 0.11 | 0.23 | -9 | -6 | -7 | 0.58 | 0.54 | 0.46 | 0.11 | 0.14 | 0.25 | 0.08 | 0.15 | 0.22 |
| P23/P25 | 0.48 | 0.20 | 0.33 | 0.53 | 0.22 | 0.37 | -7 | -6 | -7 | 0.60 | 0.40 | 0.52 | 0.41 | 0.17 | 0.34 | 0.49 | 0.19 | 0.31 |
| P24/P26 | 0.34 | 0.07 | 0.18 | 0.31 | 0.12 | 0.18 | -7 | -6 | -6 | 0.56 | 0.44 | 0.41 | 0.28 | 0.02 | 0.25 | 0.33 | 0.10 | 0.13 |
| P28/P27 | 0.18 | 0.08 | 0.14 | 0.25 | 0.10 | 0.19 | -14 | -13 | -12 | 0.70 | 0.62 | 0.52 | 0.32 | 0.12 | 0.15 | 0.31 | 0.23 | 0.25 |
| P29/P27 | 0.19 | -0.01$^{NS}$ | 0.30 | 0.15 | -0.01$^{NS}$ | 0.18 | -6 | -5 | -4 | 0.62 | 0.55 | 0.57 | 0.14 | 0.12 | 0.19 | 0.14 | 0.12 | 0.22 |
| P29/P30 | 0.18 | 0.04 | 0.30 | 0.13 | 0.05 | 0.22 | -5 | -4 | -6 | 0.47 | 0.46 | 0.53 | 0.07 | -0.04 | 0.10 | 0.06 | 0.08 | 0.08 |
| P33/P34 | 0.42 | -0.06 | 0.15 | 0.37 | -0.01$^{NS}$ | 0.17 | -10 | -4 | -4 | 0.40 | 0.16 | 0.12 | 0.21 | -0.11 | 0.06 | 0.20 | -0.10 | -0.01$^{NS}$ |
| P35/P36 | 0.15 | -0.12 | 0.02 | 0.16 | -0.11 | 0.07 | -4 | 2 | 0 | 0.43 | -0.13 | 0.08 | 0.09 | 0.00$^{NS}$ | 0.03 | 0.13 | -0.06 | 0.02 |
| P37/P38 | 0.12 | 0.46 | 0.03 | 0.29 | 0.25 | 0.01$^{NS}$ | -9 | -6 | -8 | 0.49 | 0.28 | 0.33 | 0.21 | 0.39 | 0.04 | 0.27 | 0.22 | 0.05 |
| P41/P42 | 0.03 | 0.02 | 0.24 | 0.13 | 0.03 | 0.23 | -10 | -11 | -11 | 0.61 | 0.61 | 0.57 | 0.17 | 0.25 | 0.34 | 0.16 | 0.21 | 0.31 |

$^{\dagger}$NS, not significantly different from zero ($P$ = 0.05). All other estimates of R and $r_{MP}$ were significant.

## Bibliography

Albrecht, T., V. Wimmer, H.-J. Auinger, M. Erbe, C. Knaak, M. Ouzunova, H. Simianer, and C.-C. Schön. 2011. Genome-based prediction of testcross values in maize. Theor. Appl. Genet. 123: 339–350.

Asoro, F.G., M.A. Newell, W.D. Beavis, M.P. Scott, and J.-L. Jannink. 2011. Accuracy and training population design for genomic selection on quantitative traits in elite North American oats. Plant Gen. 4:132–144.

Bates, D., M. Maechler, and B. Bolker. 2011. Welcome to lme4 – Mixed-effects models project. R Foundation for Statistical Computing, Vienna, Austria. http://lme4.r-forge.r-project.org/ (accessed 2 Dec. 2013).

Bernardo, R. 1991a. Retrospective index weights used in multiple trait selection in a maize breeding program. Crop Sci. 31:1174–1179.

Bernardo, R. 1991b. Correlation between testcross performance of lines at early and late selfing generations. Theor. Appl. Genet. 82:17–21.

Bernardo, R., and J. Yu. 2007. Prospects for genomewide selection for quantitative traits in maize. Crop Sci. 47:1082–1090.

Browning S.R. and B. L. Browning. 2007. Rapid and accurate haplotype phasing and missing-data inference for whole-genome association studies by use of localized haplotype clustering. Am. J. Hum. Genet. 81:1084-1097.

Clark, S.A., J.M. Hickey, H.D. Daetwyler, and J.H. van der Werf. 2012. The importance of information on relatives for the prediction of genomic breeding values and the

implications for the makeup of reference data sets in livestock breeding schemes. Genet. Sel. Evol. 44:4.

Combs, E., and R. Bernardo. 2013a. Accuracy of genomewide selection for different traits with constant population size, heritability, and number of markers. Plant Gen. 6:1–7.

Combs, E., and R. Bernardo. 2013b. Genomewide selection to introgress semidwarf maize germplasm into U.S. Corn Belt inbreds. Crop Sci. 53:1427–1436.

Cooper, M., and I.H. Delacy. 1994. Relationships among analytical methods used to study genotypic variation and genotype-by-environment interaction in plant breeding multi-environment experiments. Theor. Appl. Genet. 88:561–572.

Daetwyler, H.D., R. Pong-Wong, B. Villanueva, and J.A. Woolliams. 2010. The impact of genetic architecture on genome-wide evaluation methods. Genetics 185:1021–1031.

Darrah, L.L., and M.S. Zuber. 1986. 1985 United States farm maize germplasm base and commercial breeding strategies. Crop Sci. 26:1109–1113.

Dekkers, J.C.M., and J. A. M. van Arendonk. 1998. Optimizing selection for quantitative traits with information on an identified locus in outbred populations. Genet. Res. 71:257–275.

Dudley, J.W. 1993. Molecular Markers in Plant Improvement: Manipulation of Genes Affecting Quantitative Traits. Crop Sci. 33: 660-668.

Elshire, R.J., J.C. Glaubitz, Q. Sun, J. Poland, K. Kawamoto, E.S. Buckler, and S.E. Mitchell. 2011. A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. PLoS One 6:e19379.

Endelman, J.B. 2011. Ridge regression and other kernels for genomic selection with R package rrBLUP. Plant Gen. 4:250–255.

Goddard, M. 2009. Genomic selection: prediction of accuracy and maximisation of long term response. Genetica 136:245–257.

Guan, Y., and M. Stephens. 2008. Practical issues in imputation-based association mapping. PLoS Genet. 4:e1000279.

Guo, Z., D.M. Tucker, J. Lu, V. Kishore, and G. Gay. 2012. Evaluation of genome-wide selection efficiency in maize nested association mapping populations. Theor. Appl. Genet. 124:261–275.

Habier, D., J. Tetens, F.-R. Seefried, P. Lichtner, and G. Thaller. 2010. The impact of genetic relationship information on genomic breeding values in German Holstein cattle. Genet. Sel. Evol. 42:5.

Haldane, J. 1946. The interaction of nature and nurture. Ann. Eugen. 13:197–205.

Hallauer, A.R. 1990. Methods used in developing maize inbreds. Maydica 35:1–16.

Heffner, E.L., M.E. Sorrells, and J.-L. Jannink. 2009. Genomic selection for crop improvement. Crop Sci. 49:1–12.

Heffner, E.L., A.J. Lorenz, J.-L. Jannink, and M.E. Sorrells. 2010. Plant breeding with genomic selection: gain per unit time and cost. Crop Sci. 50:1681–1690.

Heffner, E.L., J.-L. Jannink, H. Iwata, E. Souza, and M.E. Sorrells. 2011a. Genomic selection accuracy for grain quality traits in biparental wheat populations. Crop Sci. 51:2597–2606.

Heffner, E.L., J.-L. Jannink, and M.E. Sorrells. 2011b. Genomic selection accuracy using multifamily prediction models in a wheat breeding program. Plant Gen. 4:65–75.

Heslot, N., H.-P. Yang, M.E. Sorrells, and J.-L. Jannink. 2012. Genomic selection in plant breeding: A comparison of models. Crop Sci. 52:146–160.

Hickey, J.M., J. Crossa, R. Babu, and G. de los Campos. 2012. Factors affecting the accuracy of genotype imputation in populations from several maize breeding programs. Crop Sci. 52:654-663.

Holland, J.B., W.E. Nyquist, and C.T. Cervantes-Martinez. C.T. 2003. Estimating and interpreting heritability for plant breeding: An update. Plant Breed Rev. 22: 9–112. John Wiley and Sons, New York.

Iwata, H., and J.L. Jannink. 2010. Marker genotype imputation in a low-marker-density panel with a high-marker-density reference panel: Accuracy evaluation in barley breeding lines. Crop Sci. 50:1269-1278.

Jacobson, A., L. Lian, S. Zhong, and R. Bernardo. 2014. General Combining Ability Model for Genomewide Selection in a Biparental Cross. Crop Sci. 54:895-905.

Jacobson, A., L. Lian, S. Zhong, and R. Bernardo. 2015. Marker imputation prior to genomewide selection in biparental maize populations. In preparation.

Jannink, J.L. 2010. Dynamics of long-term genomic selection. Genet. Sel. Evol. 42:35.

Lian, L., A. Jacobson, S. Zhong, and R. Bernardo. 2014. Genomewide Prediction Accuracy within 969 Maize Biparental Populations. Crop Sci. 54:1514-1522.

Li, Y., H.N. Kadarmideen, and J.C.M. Dekkers. 2008. Selection on multiple QTL with control of gene diversity and inbreeding for long-term benefit. J. Anim. Breed. Genet. 125:320–329.

Liu, W., M. Gowda, J. Steinhoff, H.P. Maurer, T. Würschum, C.F.H. Longin, F. Cossic, and J.C. Reif. 2011. Association mapping in an elite maize breeding population. Theor. Appl. Genet. 123:847–858.

Lorenz, A.J., S. Chao, F.G. Asoro, E.L. Heffner, T. Hayashi, H. Iwata, K.P. Smith, M.E. Sorrells, and J. -L. Jannink. 2011. Genomic selection in plant breeding: Knowledge and prospects. Adv. Agron. 110:77-123.

Lorenz, A.J., K.P. Smith, and J.-L. Jannink. 2012. Potential and optimization of genomic selection for fusarium head blight resistance in six-row barley. Crop Sci. 52:1609–1621.

Lorenz, A.J. 2013. Resource allocation for maximizing prediction accuracy and genetic gain of genomic selection in plant breeding: a simulation experiment. G3 (Bethesda). 3:481–91.

Lorenzana, R.E., and R. Bernardo. 2009. Accuracy of genotypic value predictions for marker-based selection in biparental plant populations. Theor. Appl. Genet. 120:151–161.

Lu, H., J. Romero-Severson, and R. Bernardo. 2002. Chromosomal regions associated with segregation distortion in maize. Theor. Appl. Genet. 105:622–628.

Marchini, J., B. Howie, S. Myers, G. McVean, and P. Donnelly. 2007. A new multipoint method for genome-wide association studies by imputation of genotypes. Nat. Genet. 39:906-913.

Massman, J.M., H.-J.G. Jung, and R. Bernardo. 2012. Genomewide selection versus marker-assisted recurrent selection to improve grain yield and stover-quality traits for cellulosic ethanol in maize. Crop Sci. 53:58–66.

Massman, J.M., A. Gordillo, R.E. Lorenzana, and R. Bernardo. 2013. Genomewide predictions from maize single-cross data. Theor. Appl. Genet. 126:13–22.

Meuwissen, T.H., B.J. Hayes, and M.E. Goddard. 2001. Prediction of total genetic value using genome-wide dense marker maps. Genetics 157:1819–1829.

Mihaljevic, R., C.C. Scho, H.F. Utz, and A.E. Melchinger. 2004. Correlations and QTL correspondence between line per se and testcross performance for agronomic traits in four populations of European maize. Crop Sci. 45:114–122.

Muir, W.M. 2007. Comparison of genomic and traditional BLUP-estimated breeding value accuracy and selection response under alternative trait and genomic parameters. J. Anim. Breed. Genet. 124:342–355.

Ouyang, Z., R.P. Mowers, A. Jensen, S. Wang, and S. Zheng. 1995. Custer analysis for genotype × environment interaction with unbalanced data. Crop Sci. 35:1300-1305.

Piepho, H.P. 2009. Ridge regression and extensions for genomewide selection in maize. Crop Sci. 49:1165–1176.

Purcell, S., B. Neale, K. Todd-Brown, L. Thomas, M.A.R. Ferreira, D. Bender, J. Maller, P. Sklar, P.I.W. de Bakker, M.J. Daly, and P.C. Sham. 2007. PLINK: a tool set for whole-genome association and population-based linkage analyses. Am. J. Hum. Genet. 81:559–575.

R Development Core Team. 2012. R: A language and environment for statistical computing.

Riedelsheimer, C., J.B. Endelman, M. Stange, M.E. Sorrells, J.-L. Jannink, and A.E. Melchinger. 2013. Genomic predictability of interconnected biparental maize populations. Genetics 194:493–503.

Scheet, P., and M. Stephens. 2006. A fast and flexible statistical model for large-scale population genotype data: applications to inferring missing genotypes and haplotypic phase. Am. J. Hum. Genet. 78:629–644.

Schulz-Streeck, T., J.O. Ogutu, Z. Karaman, C. Knaak, and H.P. Piepho. 2012. Genomic selection using multiple populations. Crop Sci. 52:2453–2461.

Semagn, K., R. Babu, S. Hearne, and M. Olsen. 2014. Single nucleotide polymorphism genotyping using Kompetitive Allele Specific PCR (KASP): overview of the technology and its application in crop improvement. Mol. Breed. 33:1–14.

Servin, B., and M. Stephens. 2007. Imputation-based analysis of association studies: candidate regions and quantitative traits. PLoS Genet. 3:e114.

Smith, O.S. 1986. Covariance between line per se and testcross performance. Crop Sci. 26:540–543.

Smith, J.S.C. 1988. Diversity of United States hybrid maize germplasm; Isozymic and Chromatographic Evidence. Crop Sci. 28:63–69.

Smith, J.S.C., T. Hussain, E.S. Jones, G. Graham, D. Podlich, S. Wall, and M. Williams. 2008. Use of doubled haploids in maize breeding: implications for intellectual property protection and genetic diversity in hybrid crops. Mol. Breed. 22: 51–59.

Sokal, R.R., and C.D. Michener. 1958. A statistical method for evaluating systematic relationships. Univ. Kansas Sci. Bull. 38:1409–1438.

Tanksley, S.D., and S.R. McCouch. 1997. Seed Banks and molecular maps: unlocking genetic potential from the wild. Science. 277:1063–1066.

Technow, F., A. Bürger, and A.E. Melchinger. 2013. Genomic prediction of northern corn leaf blight resistance in maize with combined or separated training sets for heterotic groups. Gene Genet. Genom. 3:197–203.

Troyer, A.F., S.J. Openshaw, and K.H. Knittle. 1988. Measurement of genetic diversity among popular commercial corn hybrids. Crop Sci. 28:481–485.

Troyer, A.F. 1996. Breeding widely adapted, popular maize hybrids. Euphytica. 92:163–174.

Windhausen, V.S., G.N. Atlin, J.M. Hickey, J. Crossa, J.-L. Jannink, M.E. Sorrells, B. Raman, J.E. Cairns, A. Tarekegne, K. Semagn, Y. Beyene, P. Grudloyma, F. Technow, C. Riedelsheimer, and A.E. Melchinger. 2012. Effectiveness of genomic prediction of maize hybrid performance in different breeding populations and environments. Gene Genet. Genom. 2:1427–1436.

Wu, R., C. Ma, and G. Casella. 2007. Statistical Genetics of Quantitative Traits: Linkage, Maps and QTL. Springer, New York.

Zhang, Z., and T. Druet. 2010. Marker imputation with low-density marker panels in Dutch Holstein cattle. J. Dairy Sci. 93:5487–5494.

Zhao, Y., M. Gowda, W. Liu, T. Würschum, H.P. Maurer, F.H. Longin, N. Ranc, and J.C. Reif. 2012. Accuracy of genomic selection in European maize elite breeding populations. Theor. Appl. Genet. 124:769–776.